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ALPHEUS HYATT AND HIS PRINCIPLES OF RESEARCH[1]

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PROFESSOR HYATT devoted his life to pure science in the best sense of the word. While known primarily for his work on fossil cephalopods, in his researches he covered a wide range of groups, doing critical work on sponges, bryozoans, pelecypods, gastropods, cephalopods and insects. He also published a number of purely philosophical papers on his subject. He taught zoology and palæontology, was a museum administrator, an organizer of societies, and maintained a seaside laboratory at Annisquam, Mass. He was fond of social life and was a most genial and charming host. With strong personal feelings and convictions, he was remarkably tolerant of differences of opinion. One of the most approachable of men, he was very kind and considerate to young men. The accompanying portrait is from a bas-relief made by Professor Hyatt's daughter, now the wife of Dr. Alfred G. Mayer.

Professor Hyatt was essentially philosophical in all his work, and his researches were largely devoted to evolutionary problems. His publications contain most important conclusions and generalizations. He discovered new principles and greatly expanded the principles of others, so that he was justly considered the founder of

[1] A paper given before the Palæontological Society of America, at the New Haven meeting, December, 1912.

a school of evolutionary research. A leader in this school was the late Charles Emerson Beecher, an eminent professor in Yale University. I wish to point out briefly what these principles are, and their application, but without going into the question of who first enunciated the principles, which is often difficult to ascertain. For the present purpose it is sufficient to consider them as the principles that Hyatt made use of and welded into a component whole for phylogenetic investigation.

It was my privilege to be intimately associated with Professor Hyatt as a student and assistant from 1886, until his death, in 1902, and I can not too strongly express the help and pleasure derived from his boundless enthusiasm, ever ready sympathy and wise counsel. He was laborious and painstaking in his work, constantly urged the importance of large series of individuals for study, and the importance of the bearing of abnormal or pathological specimens. The value of a specimen to him was for what it showed, by itself, and in its relation to associated forms. He urged the comparative study of young and adult, living and fossil forms in a united study. To a zoologist the only difference that should be recognized between living and fossil animals is the condition of preservation and the time element. A study of the recent throws light upon the fossil, and conversely a study of the fossil throws light upon the recent. A united study of both recent and fossil gives a grasp upon a group that can not be attained from either alone.

Stages in development were constantly uppermost in Professor Hyatt's mind, not stages in the embryo only, which are the main conception of stages to most zoologists, but stages throughout the life of the individual, from the egg to the adult and old age. It was the later, or postembryonic, stages that he especially urged the importance of to the phylogenist, and he demonstrated that these later stages possess characters which are directly comparable to the adult condition of related forms. In other words, that the ontogeny of the indi-

vidual gives in abbreviated form a recapitulation of the phylogeny of the group. This is the law of morphogenesis of Hyatt[2] by which he endeavored to demonstrate that a natural classification may be made by a system of analysis in which the individual is the unit of comparison, because its life in all its phases, morphological and physiological, healthy or pathological, embryo, larva, adolescent, adult and old (ontogeny), correlates with the morphological and physiological history of the group to which it belongs (phylogeny).

To the student of invertebrate fossils these animals present certain advantages, not only on account of their relative abundance, but also because, in many forms at least, from the study of a single specimen, one can gather in a more or less complete degree the stages through which it has passed in development. As Hyatt[3] says:

> How unreasonable it would seem to a student of fossil Mammalia, if he were requested to do what it would be appropriate to require from a student of fossil Cephalopoda, viz., to describe from the investigation of a single perfect fossil skeleton of an adult, not only the characteristics of the skeleton at the stage of growth at which the animal died, but the developmental stages of this same skeleton, and in case it were the remains of an old, outgrown animal, also, the retrograde metamorphoses through which it had passed during its last stages of decline. It might require a lifetime to make out the stages of a single species of mammal satisfactorily from the isolated specimens which would be found and the attempt would be hopeless for all the youngest stages of growth, while the bones were still cartilaginous. This kind of evidence, however, is readily obtainable among fossil Cephalopods . . . and it can be obtained in good collections everywhere.

While this is especially true of the tetrabranchiate cephalopods, it is also true in a more or less complete degree of some other groups of molluscs, as well as many brachiopods, echinoderms and corals.

As examples of types showing stages in development, the following may be cited. The living *Nautilus* has a close-coiled shell, but in its development passes through

[2] A. Hyatt, "Genesis of the Arietidæ," Smithsonian Contributions to Knowledge, Washington, 1889.

[3] A. Hyatt, "Phylogeny of an Acquired Characteristic," *Proc. Amer. Phil. Soc.*, Vol. 32, 1894.

arcuate, loose-coiled, then close-coiled stages directly comparable to the adults of Paleozoic cyrtoceran, gyroceran and nautiloid representatives of its own group. As shown by J. Perrin Smith,[4] the highly evolved Cretaceous *Placenticeras pacificum* which in the adult has complex sutures, in the development of these parts passes through simpler stages which are comparable to the adult structures of nautiloid, goniatitic and glyphioceran forms, followed by stages in which the septa are comparable to those of early *Ammonites,* before it assumes its adult generic features. The recent *Pecten* has strongly marked ears, but the young shell is strikingly different, first having a rounded nuculoid form, followed successively by *Rhombopteria, Pterinopecten* and *Aviculopecten* stages before its adult character is attained. In Echini the recent *Goniocidaris* and other genera, both recent and fossil, have two or more columns of plates in each interambulacral area, but in the young they pass through a stage in which there is a single plate at the ventral border of the interambulacra, which is comparable as a stage in development to the adult of the Ordovician *Bothriocidaris* which retains a single column of plates in each interambulacral area in the adult. The Lower Carboniferous echinoid *Oligoporus* which in each ambulacrum has four columns of plates with, in addition, scattered isolated plates, passes through stages with primary plates only, as in *Palæechinus,* then primary and occluded plates as in *Maccoya,* followed by four columns, without isolated plates, as in *Lovenechinus,* before attaining its generic character. In Brachiopoda, as shown abundantly by Beecher and others, stages in development are shown in the exterior and interior of the shell and the brachial supports which can be closely correlated with adult characters of more primitive representatives in the group.

While stages in development from the young to the adult are typically all progressive, in senescence, the

[4] J. P. Smith, "The Development and Phylogeny of Placenticeras," *Proc. California Acad. Sci.*, Ser. 3, Geology, Vol. 1, No. 7, 1900.

stages that appear are in the main regressive. Nautiloids and ammonoids, which are characterized by close-coiled shells, build loose-coiled or even uncoiled additions; specialized *Ammonites* with complex septa, in senescence build simpler septa. Palæozoic Echini, which are characterized by many columns of plates in an interambulacral area, lose some of these columns in old age growth, all in these features taking on simpler characters comparable to those seen in their own youth, and also comparable to the characters of adults in regressive series in their own groups.

As an aid in describing stages, Professor Hyatt[5] devised a classification of stages in development and decline which is a great convenience in exact description. In this classification the ontogeny is primarily divided into embryonic and postembryonic periods, the latter being for the most part the more important in phylogenetic work. Of embryonic stages the *protembryo* is represented by the egg and segmentation stages of the same, comparable to the simple and colonial Protozoa as adult forms. The *mesembryo* is the blastula stage, with a single layer of cells on the periphery of a hollow sphere, comparable to *Volvox* and *Eudorina*, the Mesozoa of Hyatt. The *metembryo* is the gastrula stage, comparable to the simplest of the sponges. The *neoembryo* is a later stage represented by the early ciliated cephalula stage of a brachiopod and the trochosphere of a mollusc, comparable to the embryo of chætopod worms and other Cœlomata. The *typembryo* is that stage in development when the features of the great group to which the animal belongs appear. In Mollusca the shell gland and plate-like beginnings of the shell appear at this stage. In brachiopods, two folds of the second segment of the embryo turn forward and the corneous shell begins to appear. The *phylembryo* is the completed embryonic stage and is the first ontogenetic stage that is applicable

[5] A. Hyatt, "Values in Classification of the Stages of Growth and Decline with Propositions for a New Nomenclature." [Somewhat altered in later publications. R. T. J.] *Proc. Boston Soc. Nat. Hist.*, Vol 23, 1888.

in palæontological study. It is the stage in which the characters of the class to which the animal belongs are established. This period is represented by the protechinus of Echini, the protegulum of Brachiopoda, the prodissoconch of Pelecypoda, the protœcium of Bryozoa, the protoconch of Cephalous Mollusca and the protaspis of the Tritobita. This stage in development is represented in fossil as well as living forms in many types, and the primitive radicle that it represents as a phylogenetic stage has been pointed out as *Paterina* for the Brachiopoda by Beecher, as a nuculoid type for certain Pelecypoda, and as *Bothriocidaris* for the whole class of Echini by Jackson.

Of postembryonic stages the first are the *nepionic* or babyhood stages, abundantly recognizable in fossil as well as recent types. Succeeding these are the *neanic*, or youthful stages. The *ephebic* is the adult, or that stage in which the full species characters are evinced. Senescence or old age is expressed in *gerontic* stages, in which appear the loss of characteristic species features, and by such loss an approach is commonly made to the youthful character before such features are attained. Gerontic stages while in a measure repeating youthful characters, do so in the inverse order to that in which they are acquired in ontogeny. As shown abundantly by Hyatt, senescent features are prophetic of the adult characters in regressive series of the group.

In studies of ontogeny it often occurs that stages need to be further subdivided. For this purpose Professor Hyatt introduced the prefixes *ana*, *meta* and *para*, so that one can speak of the *ananepionic*, *metanepionic* or *paranepionic* stage of *Nautilus*, etc. By means of this simple nomenclature the life stages of any organism are divisible into ten main or thirty minor periods, which are thus readily and clearly expressed.

In ontogeny, as shown by overwhelming evidence, the organism passes through stages which repeat the characters of adults of more primitive types in serial order, and it is believed that this serial order may be safely

accepted as a recapitulation of the phylogeny of the group in hand. Stages are not equally clear in all types, for stages may be skipped, or may be telescoped in specialized forms, but in primitive forms (*Nautilus, Lingula, Pecten, Cidaris*) they are astonishingly clear and complete. By some investigators stages have been denied and the recapitulation theory considered a myth. I can not enter into discussion here, but can simply say that it is felt that opponents have not considered the evidence. Cumings[6] has recently put the matter well in a defence of the Recapitulation Theory.

The principle of acceleration of development, originated by Professor Hyatt,[7] is at once an explanation of the existence of stages in development, and the loss, or skipping of stages as well. This principle maintains that features appearing at or near the adult period of development are inherited at earlier and earlier stages in successive generations until they exist only in the extreme young or are skipped as stages in development.

As examples of accelerations: In certain Palæozoic Echini the full number of columns of ambulacral and interambulacral plates are attained only in the adult. In more specialized species the similar columns are taken on much earlier in both areas than they appear in lower species (*Melonechinus*). The pelecypod *Hinnites* is attached by the fixation of one valve to foreign objects when about one fourth grown, and then loses its young pecteniform character. The allied *Spondylus* is attached when very much younger and thus earlier loses the similar stage. *Plicatula* is attached at the close of the prodissoconch stage and has lost the pecteniform stage altogether. In primitive tritobites (*Solenopleura, Sao*) the protaspis is rounded with neither dorsal eyes nor

[6] E. R. Cumings, "Palæontology and the Recapitulation Theory," *Proc. Indiana Acad. Sci.*, twenty-fifth anniversary meeting, 1909.

[7] A. Hyatt, "On Parallelism between the Different Stages of Life in the Individual and Those in the Entire Group of the Molluscous Order Tetrabranchiata," *Mem. Boston Soc. Nat. Hist.*, Vol. 1, 1866, p. 203. See also [minutes of meeting of February 21, 1866] *Proc. Boston Soc. Nat. Hist.*, Vol. 10, pp. 302–303.

ornamentation. In the specialized genera *Acidaspis* and *Arges*, as shown by Beecher, both dorsal eyes and denticulate ornamentations occur in the protaspis.

In acceleration of development, when skipping of stages occurs, it is not the earliest or embryonic stages that are skipped, but later or postembryonic. Embryonic stages are clung to with striking pertinacity. Stages are often run together or telescoped as expressed by Grabau,[8] when in a specialized type more than one phase may be represented at a single stage, although such stages are clearly distinct in more primitive types.

As an outgrowth of Professor Hyatt's studies of stages in development, the principle of colonial development has been enunciated independently by Ruedemann[9] in Graptolites, by Cumings[10] in Bryozoa and by Lang[11] also in Bryozoa. These investigators show that in the growth of the colony there are distinct stages in development which can be correlated with the adult characters of more primitive colonial forms. In this respect the colony behaves as an individual. Cumings introduces the terms nepiastic, neanastic, ephebastic, gerontastic as descriptive adjectives of these colonial stages. It is felt that this special nomenclature for colonial stages is unnecessary and therefore undesirable, because the simpler the terminology can be kept in such work, the more likely it is to be widely accepted and made use of.

Another phase of stages is localized stages in development in which I[12] showed that throughout the life of the individual stages may be found in localized parts which

[8] A. W. Grabau, "Studies of Gastropoda. III. On Orthogenetic Variation," AMER. NATURALIST, Vol. 41, 1907.

[9] R. Ruedemann, "Growth and Development of *Goniograptus thureaui* M'Coy," *Bull. N. Y. State Mus.*, No. 52, 1902.

R. Ruedemann, "Graptolites of New York." Pt. 1, *Mem. N. Y. State Mus.*, No. 7, 1904. Pt. 2, *idem*, No. 11, 1904.

[10] E. R. Cumings, "Development of Some Palæozoic Bryozoa," *Amer. Journ. Sci.* (4), Vol. 17, 1904.

[11] W. D. Lang, "The Jurassic Form of the 'Genera' *Stomatopora* and *Proboscina*," *Geol. Mag.*, dec. 5, Vol. 1, 1904.

[12] R. T. Jackson, "Localized Stages in Development in Plants and Animals," *Mem. Boston Soc. Nat. Hist.*, Vol. 5, 1899.

repeat the characters seen in youth and in the adults of more primitive types. Such localized stages are shown by many trees and other plants. In the oak, ash and hickory, suckers from the base of the tree have simple forms of leaves, comparable to those seen in young seedlings. Beneath the flower (rose, peony), at the tips of branches (hickory, sassafras) and in diseased or feeble growths (tulip-tree, red cedar) leaves often occur which in simplicity of character are comparable to those of seedlings or more primitive species in the group. Localized stages occur also in herbaceous plants as shown by Cushman.[13]

Amongst animals localized stages are shown where during growth there is an addition of similar parts as the plates in echinoderms, septa in cephalopods and in the developing zooids of colonies of corals and, according to Ruedemann, in Graptolites. In these types the parts as added present stages which are comparable to stages seen in the ontogenesis of the individual as a whole. In Echini new plates are added to the corona immediately below the oculars, and at this region throughout life the ambulacral plates are of a simple character, whereas the older earlier formed plates during their individual development may have taken on complex characters, for example, in *Centrechinus* (*Diadema*) ambulacral plates are compound, but close to the oculars are simple. In the Palæozoic family of the Palæechinidæ, the ambulacrum at the equator, or midzone, has from two to twelve columns of plates in each area, but in those genera with many columns there are only two columns dorsally in the area where new plates are added. In crinoids, in which the arms have the plates arranged in a biserial manner (*Encrinus, Platycrinus*) as shown by Grabau,[14] a uniserial arrangement exists at the tips

[13] J. A. Cushman, "Studies of Localized Stages of Growth in Some Common New England Plants," AMER. NATURALIST, 1902; *idem*, "Studies of Localized Stages in Some Plants of the Botanic Gardens of Harvard University," AMER. NATURALIST, 1903.

[14] A. W. Grabau, "Notes on the Development of the Biserial Arms in Certain Crinoids," *Amer. Journ. Sci.* (4), Vol. 16, 1903.

where the young plates are added. In *Ammonites*, as *Placenticeras*, in which the sutures of the septa are complex, often in a very high degree, we find that at the inner, or umbilical, portion of each individual septum a simpler condition exists, and greater complexity is attained in passing from the ventral portion of the septum outward, or dorsally. This simpler ventral portion in an adult can be compared with the simpler condition in a whole septum of the young, or with the septum of the adult in a more primitive and geologically older representative of the group.

Parallelism is a most important principle and was constantly used by Professor Hyatt in his studies. Parallelism is the taking on of a similar form in independent lines of descent. It may help one in explaining the origin of structures, but is sometimes confusing as indicating a basis of relationship which is misleading. In Crustacea the recent isopod *Serolis* closely resembles a trilobite. The uncoiled gastropod shell *Vermetus* closely resembles the worm *Serpula*. *Spondylus*, *Chama* and *Mülleria* amongst Pelecypoda, and *Davidsonella* and *Derbya* among Brachiopoda are all attached by the calcareous fixation of one valve and closely resemble *Ostrea*, which has a similar habit of life. The complex septa of the Tertiary nautiloid *Aturia* closely resemble those of the Devonian ammonoid *Goniatites*. Echini with imbricating coronal plates were considered as related on account of this character, but this structure appears in several independent lines in the group. The recent deep-sea Echinothuriidæ have many rows of ambulacral plates only in the peristome. By this character they have been associated with the Palæozoic Lepidocentridæ which have the same feature. I believe however that it is purely a parallelism and not a basis for genetic connection.

Larval adaptation is the term applied to special features built up as youthful adaptations and which are not, therefore, of phylogenetic significance. Such adaptations are a marked feature of certain groups as the ventral spurs developed in the embryonic glochidial stage of

the Unionidæ. Larval adaptations are most marked in the youthful stages of some insects, as in caterpillars. In most invertebrates, however, at least in postembryonic stages, larval adaptations are uncommon and can usually be eliminated as a factor in studying ontogenetic stages.

The Hyatt principles have been used as a working basis in the phylogenetic classification of three entire classes of animals, the Brachiopoda and Trilobita by Beecher[15] and the Echini by myself.[16] They have also been used as a basis of partial classifications of Cephalopoda by Hyatt himself, of Protozoa by Cushman,[17] of Pelecypoda by Jackson,[18] of Gastropoda by Grabau,[19] and also to a certain extent in suggesting genetic relationships in a number of other groups of animals and in plants by various investigators.

If I may be permitted to speak of my own studies, I have recently completed a phylogenetic study of the Echini, and throughout the work made use of the Hyatt principles. In this use there was no occasion to qualify a single one. To work out principles largely on one group (the Cephalopoda) as did Hyatt, and then to have his followers apply these principles successfully to many widely separate groups, and even to seek and ascertain facts on the basis of the implied principles, is strong evidence that he got at fundamental truths.

At present the phylogeny of invertebrates is little studied, palæontologists are largely occupied with questions of stratigraphy, and zoologists occupy themselves with other lines of work. In future, as phylogenetic work is prosecuted, I believe that Hyatt will be looked on as the master mind who pointed out the methods by which to ascertain the true phylogenetic relations of invertebrate organic forms.

[15] C. E. Beecher, "Studies in Evolution." New York, 1901.

[16] R. T. Jackson, "Phylogeny of the Echini," *Mem. Boston Soc. Nat. Hist.*, Vol. 7, 1912.

[17] J. A. Cushman, "Developmental Stages in the Lagenidæ," AMER. NATURALIST, Vol 39, 1905.

[18] R. T. Jackson, "Phylogeny of the Pelecypoda," *Mem. Boston Soc. Nat. Hist.*, Vol. 4, 1890.

[19] A. W. Grabau, "Phylogeny of *Fusus* and Its Allies," Smithsonian Misc. Coll., Vol. 44, 1904.

THE BEARING OF TERATOLOGICAL DEVELOPMENT IN NICOTIANA ON THEORIES OF HEREDITY[1]

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IT is desirable, though difficult, to atack genetic problems by both pedigree-culture and cytological methods. It is desirable because the problems are viewed from different standpoints; it is difficult because few forms are especially favorable for either kind of work. The present paper is a preliminary report upon certain characters in a species fairly desirable from each point of attack.

Among plants teratological phenomena are common, especially those known as fasciations, Masters[2] citing, in 1869, 120 genera in which they were not infrequent.

The term fasciation is a broad one and includes, from a genetic standpoint, some very different phenomena. At least two distinct kinds of variation are now emphasized in genetic work, somatic and germinal, although often it is impossible to distinguish between them except by experimental cultures. Fasciation is a phenomenon of variation in which both types occur, though the evidence on this point is not all that could be desired. All observers agree that the fasciated character is constant and heritable in such races as *Celosia cristata*[3] (cockscomb), *Pisum sativum umbellatum*,[4] *Sedum reflexum cristata*,[5] some races of *Zea mays* and *Nicotiana*

[1] Contribution from the Laboratory of Genetics, Bussey Institution of Harvard University.

[2] Masters, M. T., "Vegetable Teratology," pp. 9–21, London, 1869.

[3] De Vries, H., "The Mutation Theory," **2**: 68, 516–519, 1910; also Lynch, Irwin, "Evolution of Plants," *Journ. Roy. Hort. Soc.*, **25**: 17–31, 1900.

[4] De Vries, H., *ibid.*, p. 513, 1910. See also Lynch, I., *ibid.*

[5] Masters, M. T., *ibid.*, pp. 18–19, 1869.

[6] East, E. M., and H. K. Hayes, "Inheritance in Maize," *Conn. Agr.*

tabacum fasciata. On the other hand, many examples of fasciation are slight or severe somatic modifications, no more permanent than a swollen limb due to a bruise in our own bodies, or a bone spavin in a horse's foot, though the tissue proliferation may remain as a lasting scar. Examples of this form may be found in *Œnothera*,[7] *Nasturtium*,[8] *Picris hieracioides* and *Raphanus raphanistrum*.[9] Such modifications are imperfectly understood, but may be brought about directly or indirectly by external agencies such as bruises, culture methods and insect injuries to the initial meristem.

Aside from the work of Mendel[10] and De Vries,[11] the phenomena of fasciation have not been dealt with in the light of modern genetics. Mendel's investigations were made on a fasciated strain of pea (*Pisum sativum umbellatum*). When crossed with a non-fasciated strain the teratological character was recessive and segregated in F_2 in a simple 3:1 ratio. This result was essentially confirmed by Lock and Bateson, although environmental conditions were found by them to affect the character more than is usual in such phenomena.

De Vries failed to distinguish between fasciations strictly heritable and those non-heritable. The only con-

Exp. Sta. Bull., No. 167, and Contrib. from Lab. of Genetics, Bussey Inst. of Harvard Univ., No. 9, p. 133, Pl. XXII (*a*) and (*b*), 1911; also Emerson, R. A., personal communication, 1911.

[7] Knox, A. A., "Induction, Development and Heritability of Fasciations," Carnegie Inst. of Wash. Pub. **98**: 1–21, Pls. I–V, 1908.

[8] Knox, A. A., *ibid.*, p. 14.

[9] Molliard, M., "Cas de virescence et de fasciation d'origine parasitaire." *Rev. Gén. de Botanique*, **12**: 323–327, 1900; also Godron, A., "Mélanges de teratologie végétale," *Mem. Soc. d. Sc. Nat. d. Cherbourg*, **16**: 81–127, pp. 96–97, 1871–1872.

[10] Mendel, G. J., "Versuche über Pflanzen-Hybriden," *Verh. Naturf. Ver. in Brünn*, **10** Abh., p. I. See Bateson, W., "Mendel's Principles of Heredity," pp. 322, 328, 330, Cambridge Univ. Press, 1909.

[11] De Vries H., *ibid.*, III, "The Inconstancy of Fasciated Races." pp. 488–526, 1910; "Monstruosités héréditaires offertes en échange aux Jardins Botaniques," *Bot. Jaarboek*, **9**: 62–93, 1897; "Over de erfelykheid der fasciatiën. Avec un résumé en langue française," *Bot. Jaarboek Dodonaea*, **6**: 72, 1894; "Sur la culture des monstruosités," *Comptes Rendus*, **128**: 125, 1899; "Sur la culture des fasciations des espèces annuelles et biannuelles," *Rev. Gén. de Bot.*, **2**: 136, 1899.

stant fasciated race[12] with which he worked is the cockscomb and his experimental researches on this plant led him to conclude that "complete atavists," or normal plants carrying the fasciated character in a latent state, are very rare, and even under repeated selection are to be obtained in very small numbers. Further, the normal plants thus obtained do not breed true, but revert very soon to the abnormal condition. While investigations have not been made showing definitely that many of De Vries's fasciations were not heritable, but were simply somatic modifications, enough evidence is at hand from numerous sources to justify at least the expression of a strong doubt of their heritable character. According to the observations of Knox, fasciated stems in Œnotheras are not germinal in origin, but traceable directly, in most cases, to insect injuries. Observations by Molliard on *Raphanus* and *Picris* support this conclusion, while Godron was unable to secure fasciated individuals from the seeds of a *Picris* plant thus affected. The fact that fasciation appears in every generation of *Œnothera* plants in varying percentages, in certain cultures, especially those of a biennial nature, is best explainable on a re-infection basis. Spiral torsion races such as *Dipsacus sylvestris torsus* in De Vries's cultures behaved, from a genetic standpoint, in the same manner as his fasciated races. Races of *Dipsacus* species are rich in torsions in Holland and Denmark, but, according to Johannsen,[13] the seeds of torsus strains when grown in England produced normal progeny. This would indicate an environmental rather than a germinal basis as a causal factor.

In all of De Vries's experimental cultures of fasciated races (with the exception of *Celosia*) only a certain per cent. (averaging in most races 50 per cent. or less) of the individuals in each generation possessed the abnormality, and he was never able to breed a constant and

[12] Possibly *Geranium molle fasciatum* may be an exception in which more than one unit factor is responsible for the anomaly. Otherwise it should have bred true at least by the sixth generation if the seed sown each year was from carefully guarded plants.

[13] Johannsen, W., public lecture IV, Boston, 1911.

genetically pure race. Even though he had been able to do this, doubt could still be cast upon the belief that he was dealing with a strictly heritable character, because the only method that seems to preclude doubt is crossing with the normal and securing the F_2 ratio. This method would eliminate the suspicion that minute bacterial or even ultra-microscopic organisms were acting as causal agents.

Emerson and East in their maize studies have obtained races breeding constant for fasciated ears. I have myself examined such a race in Emerson's cultures. Hus, on the other hand, with the same sort of an abnormality in the same plant species, *Zea mays*, secured results similar to those of De Vries.[14] Is the difference in results due to methods or to the nature of the plant abnormality itself? I shall consider the results of De Vries and others holding similar opinions in greater detail in a later paper, as such results entail an extended review.

The Problem and the Material

The problem to be discussed briefly in this paper is the relation of the cytological phenomena in the reduction divisions to certain segregating Mendelian characters, and the nature of these characters in development and inheritance.

The material upon which the study is largely based is a fasciated variety of *Nicotiana tabacum*. Although fasciations are very common in many genera and not infrequent in others, they have never been recorded (so far as I can determine) in *Nicotiana*. The present race was obtained from the selfed seed of a mutant found growing in a field of Cuban tobacco in the district of Partidos, near the town of Alquiza, Cuba, in 1907. I am indebted to Dr. E. M. East and to Mr. J. S. Dewey[15] for

[14] Hus, H., and Murdock, A. W., "Inheritance of Fasciation in *Zea mays*," *Plant World*, **14**: 88–96, 1911.

[15] Mr. J. S. Dewey is superintendent of the United States tobacco plantation belonging to the same company that controls the Cuban plantation near Alquiza.

data on this race, prior to the summer of 1910. The sport is characterized by a flattened, fasciated condition of the stem and floral structures, and a consequent increase in the number of leaves. The original mutant is described by Dewey as possessing 152 leaves on the main stalk, flowers abnormal, stem fasciated. When the abnormal plants were studied in more detail, many smaller teratological features were found, and these were especially plentiful in connection with the floral structures. The pistil frequently was incapable of functioning, because of various forms of tissue proliferation in the region of the stigma. The style was often shortened, coiled or fused near its base with an anther (staminody of the pistil). The ovary locules were very much increased in number, ranging from two (extremely rare) to as high

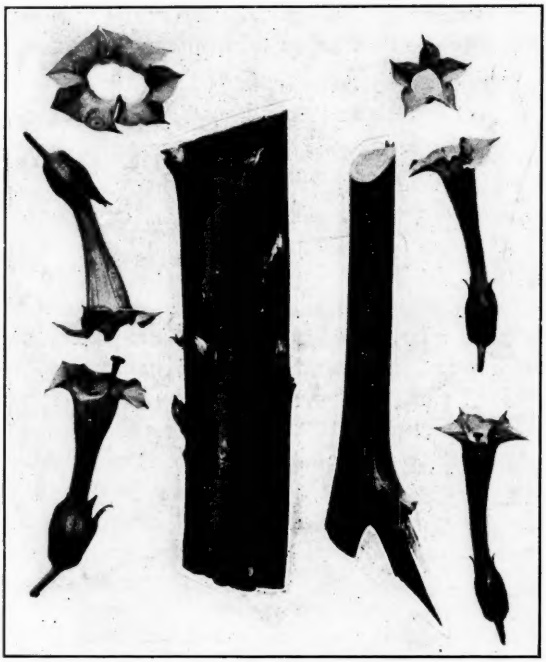


FIG. 1. Stems and flowers from the abnormal and normal strains of N. tabacum.

as twenty. Very often two or even three distinct pistils were formed in the same flower, all of which in some cases could function. The stamens were affected in both filament and anther. The filaments were often coiled, twisted, shortened or fused to the corolla. In rare cases, they were petaliferous. The anther deformities consisted of split anthers, anthers with small pistils growing from them—two or three to an anther being present in one case (pistillody of the anthers). The number of pollen sacs varied from the normal four to six.

The corolla and calyx were often split, and the lobes of the calyx and not uncommonly of the corolla, were irregular in size and shape. Occasionally the calyx and corolla merged into each other by a spiral twist. Two flowers sometimes were enclosed by the same calyx. Once or twice flowers have been found consisting of only a corolla and a few stamens, growing on the side of the normal corolla and partly fused with it. The corollas never show a doubling phenomenon to accommodate the increase in petal number but the circumference of the flower is extended, and very often these flowers are as regular and symmetrical as those of the normal. Two cases of leaves fused at the base have been found and the phyllotaxy is altered and irregular. The fasciated plants when young are practically indistinguishable from the normal. The anatomical features have not been investigated sufficiently for a report upon them at this time, and it is possible that differences between the normal and abnormal seedlings will be found when this part of the study is completed.

Five generations of the abnormal strain have been grown, amounting in all to over a thousand plants, and each individual plant has possessed the unmistakable characters of the original mutant. The monstrous character is, however, a variable one, since the stems may be extremely flattened throughout the greater part of their length or only flattened and fasciated toward their apical ends. Other characters, as already implied, fluctuate between extremes, depending in part on environment

A COMPARISON OF CERTAIN CHARACTERS OF THE F_1 AND F_2 GENERATION OF

303–1–12 is a type of extreme abnormalness. 301–1–2 represents the extreme *tabacum*. (304 × 402)–1–10 = normal F_2 segregate. (304 × 402)–1–12 = abnormal heterozygous F_2 segregate similar to the F_1 (304 × 402)–30.

		Stem	No. of Leaves	Height, In.	Flower	1	2	3	4	5	6	7	8
♀P	303–1–12	V. abn.	69	76	Sepals ..	7	6	6	7	6	8	9	7
					Petals ..	12	9	6	10	11	12	11	13
					Stamens	12	12	7	12	8	13	11	12
					Ovary locules.	3–3–3	3–3	4	3–3–2	4–3	4–4	3–3	6–3
	301–1–2	N.(?)	33	68	Sepals ..	6	6	7	6	7	6	6	6
					Petals ..	7	6	7	7	8	8	7	7
					Stamens	7	6	6	7	7	7	7	7
					Ovary locules.	3	3	3	3	3	3	3	4
♂P	402	N.	24	72	Normal as in (304×402)–1–10								
F_1	(304×402) –30	N.(?)	26	87	Sepals ..	6	6	7	6	6	6	5	6
					Petals ..	7	6	7	6	5	6	5	7
					Stamens	7	6	7	6	6	6	5	7
					Ovary locules.	3	3	3	2	2	3	2	2
F_2	(304×402) –1–10	N.	24	75	Sepals ..	5	5	5	5	5	5	5	5
					Petals ..	5	5	5	5	5	5	5	5
					Stamens	5	5	5	5	5	5	5	5
					Ovary locules.	2	2	2	2	2	2	2	2
	(304×402) –1–12	V. abn.	80	75	Sepals ..	10	12	6	8	10	7	8	9
					Petals ..	12	20	8	12	15	8	21	12
					Stamens	16	15	7	8	12	7	18	12
					Ovary locules.	6–10	6–3–4	5	3–3	3–4	4	6–4–2–2	4–3
	(304×402) –1–34	S. abn.	63	75	Sepals ..	8	7	7	7	7	6	6	6
					Petals ..	8	8	7	7	7	7	7	8
					Stamens	7	8	7	7	8	7	7	8
					Ovary locules.	3	3	3	3	4	3	3	3
	(304×402) –1–6	N.(?)	32	75	Sepals ..	5	6	6	6	7	5	6	6
					Petals ..	5	6	6	6	7	5	7	6
					Stamens	5	6	6	6	7	5	7	6
					Ovary locules.	2	3	2	3	3	3	3	3

[16] Double flower.

ABNORMAL × NORMAL *Nicotiana* (304×402) WITH THOSE OF THE PARENT STRAINS

variation of the abnormal characters toward the normal. 402 is the normal *N.* F_2 segregate. (304 × 402)–1–34 = heterozygous F_2 segregate. (304 × 402)–1–6 =

9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
8	7	7	6	7	7	6	6	6	8	8	7	6	6	7	7	7	
11	12	11	10	8	8	7	9	9	16	8	10	7	7	11	7	11	
11	14	11	12	9	8	7	11	8	17	9	12	7	6	11	7	11	
3–3	4–6–4	5–3	3–4	3–3	5	4	3–2	4–4	8–5	5	2–4	3	3	3–1	3	3–3	
8	7	6	7	8	7	6	6	6	6	6	7	7	6	6	6	6	8^{16}
8	7	8	7	8	8	9	8	7	7	7	7	8	7	8	8	5	7
10	7	6	7	7	7	8	9	7	6	6	7	7	6	8	7	5	7
4–2	4	3	3	4	3	3	2–3	4	4	3	3	3	3	4	3	3	3

Normal as in (304×402)–1–10

5	7	7	6	6	6	6	6	6	7	6	5	5	5	5	7	5	
5	7	6	6	7	6	6	7	6	7	6	6	6	5	6	7	7	
5	7	6	6	6	6	6	7	6	7	6	6	6	5	5	7	7	
3	2	3	2	3	3	3	3	3	3	3	3	3	2	3	3	2	
5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	
5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	
5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	
2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
7	8	8	12	7	10	6	7	8	8	7	7	7	7	8	7	8	
10	9	18	24	12	15	8	8	10	15	12	15	8	8	9	12	8	
7	9	16	24	8	18	7	7	6	15	8	10	7	8	8	10	8	
3	4–3	4–4–4–3	7–6–4–4	4	4–4–2	3	4	3	5–3	3–2	4–3	4	5	4	3–4	3–2	
8	7	8	9	8	7	8	7	8	7	12	9	8	8	8	12	11	
8	7	7	11	8	7	8	7	9	7	16	12	11	14	8	12	18	
7	7	8	10	7	7	7	7	9	7	16	12	11	14	7	12	15	
4	3	4	4–4	3	3	3	3	4	4	4–6–4	4–3	4–4	4–4	2	2–2	4–5–4	
5	5	5	5	6	6	6	6	6	5	5	5	5	6	6	5	6	
6	6	5	6	7	7	6	6	6	6	7	6	7	7	7	5	7	
6	6	5	6	6	7	6	6	6	6	6	5	7	6	6	5	7	
2	3	2	3	3	3	4	3	3	3	3	3	3	3	3	3	3	

and in part on the *innate* nature of the character itself. One may confuse this fluctuation to the arc made by a swinging pendulum. The arc through which the pendulum can swing is limited, but within those limits the arc may be medium, large or small, depending on the agencies that set the pendulum in motion. Agencies very different in nature may produce the same result. The pendulum is the material body which makes the arc recognizable as an entity, and in this simile may be compared to the gene for fasciation. When the pendulum is motionless, there is no arc, and there would be no fasciation if the gene remained potential.

A more definite idea of the characters of the plant and their variability may be secured by consulting the table on page 212. It should be stated that plants have been grown under many environments and with many variations in culture. But so far as our present interest goes, no very great changes have resulted. The race has always been clearly distinguishable in the adult state from the normal, whether grown under cramped greenhouse conditions, or out-of-doors; whether surrounded by a Cuban or a New England environment. No especial care, such as De Vries prescribes, regarding culture and transplantation has been given, and yet the anomaly has always bred absolutely true and no "atavists" have appeared.

The normal Cuban variety from which the fasciated strain arose is characterized by a normal round stem, regular phyllotaxy, flowers with five petals, sepals, stamens and a two-loculed ovary. The number of commercial leaves varies between 20 and 25, all leaf counts in the present investigation, being made by the commercial method.[17] Fertility is practically 100 per cent. Occasionally among hundreds of flowers examined a flower is found with an extra sepal or petal, otherwise abnormalities are unknown in our cultures of the normal variety.

[17] All leaves were recorded up to the first leafless branch ("bald sucker"), exclusive of the first three basal leaves.

In the cultures at the Bussey Institution of Harvard University the normal Cuban is known as 402: the fasciated strain as 300–309, the range in numbers representing an attempt at selection.

Methods

Data were collected on each plant and tabulated separately. The characters noted were, extent of fasciation in the stem; number of leaves, petals, sepals, stamens and ovary locules. Twenty-five flowers were taken from each plant and the parts of each flower recorded separately. In all crosses made the flowers were castrated in the bud and bagged. Pollen was taken only from anthers still in the closed bud and 95 per cent. alcohol was liberally used after each operation on hands and instruments. The Webber system of recording the plants by number was used. All seed was sown in sterilized soil and all possible care taken to avoid mixtures.

Experimental Work

Numerous crosses were made between distinct species and the abnormal race, but all of the progeny were sterile, though the abnormal character was visible in their flowers and in the increased number of leaves which they bore.

Four crosses were made between normal *N. tabacum* varieties and the abnormal, all of which produced fertile F_1 plants. The most interesting of these is a cross of the abnormal with the normal Cuban variety from which it mutated. Three generations of this cross (304×402) have been grown. The F_1 generation consisted of 39 plants, the F_2 of 97 and the F_3 of 647, totaling 783 individuals. The F_1 was intermediate in character between the two parents, as the table will show. The F_2 gave the three expected types in the ratio of 1:2:1, the actual numbers being:

	Normal	Heterozygote	Abnormal
Actual	28	52	17
Expected	24	48	24

The F_2 selections gave the results expected in F_3. Counting the total progeny (248) from F_1 and F_2 heterozygotes, the figures are:

	Normal	Heterozygote	Abnormal
Actual	68	124	56
Expected	62	124	62

The F_2 heterozygotes were in appearance duplicates of the F_1 individuals and after a little experience could be easily distinguished from the abnormal homozygotes. Clean segregates were obtained from the heterozygous

FIG. 2. F_2 segregates from the abnormal × normal (304 × 402) Nicotiana. Abnormal homozygote, heterozygote and normal homozygote. The grandparents in appearance are duplicates of the two homozygotes

plants in both F_2 and F_3 and the homozygous normals and abnormals obtained in this manner bred true in F_3 and F_4. Not being satisfied that only one factor represented the difference between the normal and the abnormal, I thought that it might be possible, through selection, to secure a normal strain from the abnormal, or at least to modify the unit character, as Castle and his students appear to have done with the hooded pattern in rats.

Selection work was started by selecting from the cultures the most abnormal and the least abnormal plants as seed producers. The work was carried through two generations with no prospect of success and there it remains at present. Progeny of the least abnormal plants were as much fasciated and otherwise abnormal as the original parent strain growing beside it. And one could not distinguish the least abnormal from the most abnormal strain except by the label. So far as the work has progressed, this fasciated strain seems no more amenable to selection than the cockscomb with which De Vries worked, and of which he said "at present at least there seems not to be any prospect of obtaining a pure atavistic strain."[18]

From a comparison between the drawing in Gerarde's Herball of 1597[19] and certain woodcuts from old horticultural magazines with the plants as they are to-day, it does not appear that much change has taken place in the cockscomb fasciation since its introduction into Europe in 1570.

The changes in the expression of the comb that gardeners and florists will maintain have taken place as a result of selection can all be accounted for by the influence of the environmental factor.

Lock planted seeds of very slightly fasciated individuals of the F_2 generation of normal $\times$ fasciated stem in *Pisum*. The F_3 plants were almost, if not as much fasciated, as the original grandparent strain.[20]

[18] De Vries, H., "The Mutation Theory," **2**: 519, 1910.

[19] Gerarde, John, "Herball or Generall Historie of Plantes," 1st ed., pp. 323–325, Fig. on p. 323, 1597. [20] Lock, R. H., *loc. cit.*, p. 106.

This fasciated strain of pea (Mummy Pea or *Pisum sativum umbellatum*) would appear to have been a very constant race, at least since 1597, when it was figured in Gerarde's "Herball."[21]

From the results of hybridization and selection, one may draw the conclusion that the fasciated mutant differed from the normal parent strain by only one factor and that it represents a mutation upon the variability of which selection has no modifying effect. The character itself appears to be due to one underlying cause and its variableness is only the external manifestation of the capricious working of that cause.

After completing a satisfactory study of the gross aspects of this character, a cytological investigation was made, with the hope that here might be found a clue to the cause or causes underlying the appearance of the anomaly.

CYTOLOGY

Much trouble in fixing material was caused through the presence of resinous substances in the tissues. Flemming's medium and strong solutions were finally found to be the most successful, although prolonged bleaching of the sections with H_2O_2 was necessary to eliminate the blackening. Care had to be exercised to secure quick penetration, as poor fixation and shrinkage were likely to result after a bath of over 24 hours. The preparations were stained in Heidenhain's iron hæmatoxylin and counterstained with clove oil saturated with erythrosin. This combination usually gave the best results —a deep black chromatin stain against a brilliant red background. Preparations were also stained with the safranin-gentianviolet-orange G combination of Flemming and restained with iron hæmatoxylin. This method gave very sharp outlines, not easily obtainable in some phases, when the ordinary hæmatoxylin method was used. Another combination which was found valuable in cases where the chromosomes were closely crowded

[21] Compare with photograph in Darbishire, A. D., "Breeding and Mendelian Discovery," p. 22, Fig. 8, 1911.

together, as in certain metaphases, is safranin, magdala red and azure II. Large quantities of the fresh material of the anthers in various stages of maturity were stained with methyl green and microscopically examined. In most cases one anther of a bud to be fixed was inspected in this manner. This precaution was necessary as a check on the occurrence of artifacts from fixation.

Briefly, conditions in the normal Cuban variety (402) are as follows. The ordinary maturation processes are those cytologists have so often described for plants, and need no recapitulation here. The spireme in prophase is single and, just preceding diakinesis, breaks up into segments which take the form of twisted and horseshoe-shaped loops. The latter resemble Davis's figures for *O. grandiflora*.[22] Each loop consists of two spireme segments joined at one end, which in the later heterotypic phases separate and go to opposite poles. Each segment is interpreted as a somatic chromosome, and the members of a pair are homologues. The other phases present nothing peculiar. The homotypic chromosomes appear as entities first in very late anaphase of the first division. The reduced chromosome number, as determined by very numerous counts of heterotypic metaphases and anaphases, and homotypic telophases is 24, the $2n$ being 48. The somatic number ($2n$) was determined by adding together the homotypic telophase chromosomes of a tetrad and dividing the entire number by two. Polar views of the metaphase of the first division in sections of 10μ have repeatedly shown the 24 gemini, each geminal chromosome consisting of a diakinetic pair. Variation of chromosome number in these normal (402) anthers is very rarely, if ever, to be found. None was found in the present investigation. Irregular divisions are not common, although occasionally one sees lagging chromosomes. Usually the phases of a single pollen sac

[22] Davis, B. M., "Cytological Studies on *Œnothera*. I. Pollen Development of *Œnothera grandiflora*," *Ann. Bot.*, **23**: 551–571, Pl. XLI, Figs. 31, 34, 36, 1909.

are more advanced at one end than at the other and the maturation processes are at a similar stage in the different sacs of the same anther. Cursory examination of reduction phenomena in the ovule confirmed these observations.

Many anthers of the abnormal (300–309) when examined cytologically, were entirely normal in all their phases of maturation. Others showed evidences of almost total sterility through premature breaking down of the archesporial tissue, while still others were only partially sterile. Anthers of this strain were mentioned earlier as sometimes having more than four pollen sacs. In such cases the maturation phases were in very different stages in the different sacs. In one sac the archesporium might be in early prophase, while in other compartments there would be almost mature pollen. This extreme variation in maturation was not confined to anthers with an abnormal sac number, but was often true of those normal in this respect. Conditions in the anthers of the abnormal strain are similar as regards the normal cytological phenomena, but various abnormalities are not uncommon. These manifest themselves in such a manner that one can not avoid believing that some subtle agent is at work here, too, distorting the internal as well as the larger so-called external characters. In both reduction divisions in all the strains examined, various abnormal phenomena are to be found which are not due to fixation or other technical operations. Contrasted with the normal (402) the maturation phases in different sacs of the same anther may be far apart. Nearly mature pollen is present in some sacs, while others in the same anther may not have progressed farther than diakinesis. Pollen tetrads are often rare in nearly mature anthers. This is true of at least five per cent. of those examined. Mother-cells may break down during early prophase, diakinesis or any of the later phases. In early prophase, the nuclear membrane may disappear and the whole archesporium disintegrate.

Again, I have found that in some sacs most of the archesporium has broken down, but some few cells seem to have escaped destruction and matured. The metaphase, so far as I have observed, is not so likely to be disturbed. An occasional premature splitting of the chromosomes takes place, increasing the number to be seen in the polar view of the nuclear plate. These are rare, but they have been observed in both the abnormal strain and the abnormal segregates. This feature has been referred to as a premature splitting,[23] but it may be interpreted as an actual increase in number such as Wilson found in *Metapodius*,[24] Stevens in *Diabrotica*[25] and Strasburger in *Wikstroemia*.[26]

In one pollen mother-cell, 51 chromosomes were clearly distinguishable, but disintegration had already commenced. In another case 30 were counted, the mother-cell appearing perfectly normal, although in the anther containing it irregular divisions were taking place. The nuclear metaphases in which such an increase in number can be seen are rare, but so far as I have observed, and I have counted many nuclear plates ideal for such work, they only occur in the abnormal or in the abnormal segregates. The heterotypic anaphases of the abnormal often show the chromosomes lagging or distributed promiscuously over the spindle. In only one case so far have I found irregular conditions in the telophase and this only in the case of one mother-cell. Counting is unsatisfactory in the anaphase of the first division, as the nucleus is small and the chromosomes are many.

Irregular divisions are present in the homotypic, but most of the abnormalities occur during the heterotypic mitosis.

[23] Preparatory for the homotypic division.

[24] Wilson, E. B., "Studies on Chromosomes. V. The Chromosomes of *Metapodius*, a Contribution to the Hypothesis of the Genetic Continuity of Chromosomes," *Journ. of Exp. Zool.*, **6**: 147–205, 1909, 1 plate and 13 text figures.

[25] Stevens, N. M., "Further Observations on Supernumerary Chromosomes, and Sex Ratios in *Diabrotica soror*," *Biol. Bull.*, **22**: 231–238, figs. 1–13, 1912. [26] Strasburger, E., "Chromomenzahl," *Flora*, **100**: 1910.

It is impossible to say whether pollen grains capable of functioning ever result from those divisions where the chromosomes are irregularly distributed. The irregularities in reduction do not produce supernumerary pollen grains, such as have been described by Juel and Strasburger for *Hemerocallis,* for in all tetrads mature enough to show the separation of the pollen grains I have always counted four. One might expect an increase in number of pollen grains formed by one mother-cell, judging from the grosser manifestations of this abnormal factor. Functioning pollen is formed in quantity and no trouble at all is found in securing plenty of selfed seed of the abnormal strain.

Reduction phenomena in the ovule of the abnormal have so far been given only a superficial examination and the observations are not complete enough to report. Observations on the ripe capsules of selfed plants would lead one to believe that here, as in the case of the pollen, partial sterility is present, due to the abortive development of the ovules, but the latter is only a supposition, which further cytological study may or may not support.

Cytological examination of the anthers of the three classes of plants obtained from the abnormal $\times$ normal (304 $\times$ 402) was made. The conditions in the reduction divisions of the normal and homozygous abnormal segregates are identical with those present in the two grandparents. The heterozygote differs from the pure abnormal in degree only, having fewer sterile anthers and other abnormalities. Otherwise what has been said of the pure abnormal (300–309) applies also to the heterozygote.

In connection with this cross, it is interesting to note what bearing the nature of the reduction divisions in the ovule (300–309) might have upon the F_2 ratio. The abnormal class, although within the probable error, is always deficient. This is true also in the fasciated peas with which Mendel[27] worked and in one race of peas hav-

[27] *Loc. cit.*

ing sterile anthers with which Bateson[28] experimented. While the number of plants has not been large in any of these cases, one wonders why it is always the abnormal (pure) class which is deficient. If the reduction phenomena in the ovules of the abnormal *Nicotiana* agree with the conditions present in the anthers, it seems not unreasonable to believe that there may be a relation between the mortality of the gametes carrying the factor for abnormalness and the deficiency in the ratio. Increased mortality of this class of gametes over the normal class would reduce the chances for combinations of the abnormal gametes, and as a consequence the normal and heterozygote combinations would be increased.

Summary of Observations

Concluding, one must bear in mind that the facts so far obtained seem to warrant the belief that some agent is at work on the internal structure as well as on the so-called external, and is of such a nature as to produce abnormalities in cell structure as well as in cell complexes or plant organs. The data, as a whole, raise a question as to the significance of chromosomes in inheritance.

Two strains of *Nicotiana tabacum* have been investigated, one being a sport from the other. The sport has been shown to differ from the normal in the possession of a unit character due to one Mendelian factor. When it is crossed with the normal, there results in F_2 a simple Mendelian ratio of 3:1 as regards normal and abnormal characters. The heterozygote is, with a little practise, distinguishable, making the ratio 1:2:1 with abnormalness partially dominant. The F_3 generation has proved these segregates to breed true. *Absolutely* clean normal segregates appear in F_2 and breed true. The abnormal character has been described in detail, and shown to affect practically all the structural parts of the plant individual, even to the germ cells. Both strains have the same chromosome number, 48 and 24, as a definite mode.

[28] Bateson, W., and others, Reports to the Evol. Com., II, p. 91, 1905.

CHROMOSOMES IN RELATION TO MENDELIAN FACTORS AND A PHYSICAL BASIS OF INHERITANCE

Suppose we maintain the factor for the abnormal condition to be a particle of one chromosome. Gametes of the abnormal strain all contain the factor for abnormalness, as reciprocal crosses with the normal give the same results. In a cross a pollen grain of the abnormal strain unites with an egg of normal (402) parentage, and an intermediate is produced in F_1. The chromosome containing the factor for abnormalness is partly neutralized by pairing with a normal homologue. Gametes of two kinds are formed in approximately equal numbers in F_1, those containing the factor for abnormalness and those without it. But on a chromosome hypothesis, how are these gametes formed? There are two reduction divisions and 48 chromosomes, 24 of abnormal parentage and 24 of normal. According to current cytological investigation and interpretation, each chromosome separates from its homologue in its entirety during the first reduction division, so that, eventually, two kinds of gametes are formed as regards chromosomes. The factor for abnormalness or fasciation is in one chromosome, and chromosomes are believed to be in homologous pairs —one maternal with one paternal. The chromosomes of a homologous pair separate during the heterotypic anaphase, one going to each pole, it being contrary to current interpretation to believe that both members of a pair may go to the same pole. On this basis, according to the law of chance, approximately half the nuclei at the end of the heterotypic division will contain the chromosome carrying the factor for abnormalness and from half it will be absent.

Experimentally it has been shown that we have been dealing with only one pair of unit characters and that no complications are present. The various crosses have always given uniform results in F_1, even between species, and the fertile cross has given a close 1:2:1 ratio in F_2. Logically, then, one is led to believe that one out of the

24 chromosomes of abnormal parentage, and only one can contain the factor for abnormalness and produce the experimental results. If more than one contained it, the ratio in F_2 would be changed. For example, if it were present in two chromosomes, the ratio (as suggested by Emerson)[29] must be 15:1 or in this particular case where the heterozygote is distinguishable, 7:8:1. We might postulate its presence in all 24 chromosomes and believe, as Cannon[30] did, that parental chromosomes separate as a phalanx in the F_1 reduction division, each group going to one pole and thereby bringing about the formation of pure parental gametes. But the cytological investigations of Sutton, Rosenberg, Strasburger and others have brought to light evidence which precludes such a supposition. The experimental data from genetic researches are also opposed to this hypothesis, if one attempts to show a relation between the reduction division and Mendelian segregation. On a chromosome hypothesis, then, one *must* believe the factor for abnormalness to be present in only one chromosome out of the 48 concerned in the F_1 reduction phenomena, in order to be in agreement with the experimental results. This being the case, how is one to account for the abnormalities which occur during the reduction divisions in the anthers of the F_1 heterozygote? For they affect, not alone one chromosome, but all the nuclear and cell material concerned in the formation of the pollen grains. Can one postulate the influence of one chromosome to be so great, at times, as to bring destruction to its 23 associates of abnormal parentage, its 24 associates of normal parentage, as well as all the other organized contents of the mother-cell? Why, it may well be asked, if this destruction is the result of the activity of one chromosome does not it take place in the case of every anther and of every pollen mother-cell? Why should it affect only two or three

[29] Emerson, R. A., "Genetic Correlation and Spurious Allelomorphism in Maize," 24th Ann. Rpt. Nebr. Agr. Exp. Sta., pp. 59–90, 1911.

[30] Cannon, W. A., "A Cytological Basis for the Mendelian Laws," *Bull. Torr. Bot. Club*, **29**: 657–661, 1902.

anthers in a flower containing 8 or 10? Not because it is absent from the other anthers, because the pollen from these anthers transmits the character. It is not a question of segregation then, but one of environment.

Evidently the gene is inactive or latent, for we know there is something present which for convenience we call a gene, and yet we can not see any of the visible signs of its presence, such as we see in the affected anthers. On a morphological conception it must be there; physiologically for the time being, so far as we can determine, it is non-existent. The inactivity we may suppose is due to a lack of a properly adjusted environment. This proper adjustment is only true of a few anthers in the F_1 plants. We believe this scarcity to be due to two kinds of latency —inactivity of the gene as in the pure abnormal and inactivity of the gene because of association with the cell materials that trace their lineage back to the sperm of the normal father. But latency is a vague term. In genetics, it is used to describe the period between the disappearance of a character and its reappearance. By pushing this conception to its logical conclusion it is clear that one can practically never prove the origin of a new character. Fasciation, while new to *Nicotiana,* is phylogenetically an old character. The production of purple fruits in *Rosa* would mean, phylogenetically, the reappearance of a latent character, for purple fruits are common to the *Amelanchiers* and to a species of *Pyrus.*[31]

The characters of the whole plant kingdom would be in a state of latency and patency, of inactivity and activity. To determine whether a character were new or not would involve a canvass of that part of the plant kingdom phylogenetically older than the family under investigation. Of course, we speak of segregation in phylogenetical lines, but the term has a different meaning in such cases. My F_2 normal segregates are pure and will breed true for absence of abnormalness, I believe, for any number of generations unless a new muta-

[31] *Pyrus Niedwetzkyana.*

tion occurs. These recurrent mutations, Johannsen says, are rare in his experience, but they are admitted to occur in almost any long-continued pedigree line, and if fasciation should appear as a repeated mutation after 20 generations of plants involving 2,000,000 individuals had been grown, is one to infer that the gene was present all this time, but latent or inactive? Or is this a new gene produced by the same condition that brought about the original fasciation? Logically, if one defends the latency conception, he must believe that the original gene for fasciation was inactive in all these millions of plants, which in our present stage of knowledge is a ridiculous assumption, since the term is used to describe a somatic appearance. Applied to genetic problems in general, hopeless chaos would result. But on the supposition that a portion of a chromosome is responsible for the abnormality, it seems to me necessary to assume the chromosome to be capable of becoming active or latent without cause. For it seems probable that the anthers are all alike from a constitutional standpoint. How else can one account for the normal anthers and the abnormal ones, the normal pollen mother-cells and those affected by the abnormality?

The conception of latency is not necessary in the case of complete or incomplete dominance in F_1 hybrids, for in such cases there is evidence that a gene from one parent may be partially or completely inhibited in its expression by factors from the other parent, and this is probably what happens when we bring a line of chromosomes and cell materials from the normal (402) plants and associate them (by fertilization) with a line of cell materials from the abnormal (300–309).

While the phenomena of segregation described in the preceding pages may be capable of interpretation on a morphological basis, the gene for fasciation appears to me to lie deeper in sporogenesis than chromosomes. The abnormal character development appears most easily interpreted from a physiological standpoint. In

F_1 there is no break in the continuity of its manifestations between sporophyte and gametophyte, even though reduction and probably segregation have occurred. And should we not expect to see such a break if segregation by chromosomes took place in sporogenesis?

The evidence as a whole I think, warrants one in the suggestion that chromosomes are characters of the zygote and gametophyte, on the same footing in development with other plant characters. It is more difficult to comprehend this conception of these bodies, because they appear as characters in the development of the cell, rather than in the development of the larger unit, the individual organism. They are characters in the sense that they disappear and reappear at a place and time in the life history of the organism which we can predict. They can be transferred from one race of organisms to another provided fertile F_1 hybrids are possible. They are influenced in as definite a manner, by the underlying cause represented by the term factor for abnormalness, as are the zygotic expressions included in the word fasciation.

Concluding, I realize these speculations are largely negative in character, but they are in accord with a steadily growing skepticism among students of genetics as to the importance of chromosomes in inheritance, and their relation to segregating Mendelian characters. The impression has been distinctly gained from a study of this abnormal strain and its crosses with the normal that chromosomes are not the omnipotent creators of destiny, but characters on the same footing with other structures. The same dynamic forces, whatever they are, are changing and modifying these chromosome characters in the same capricious manner as those of a grosser nature. One would be inclined to ascribe these changes to an ultra-microscopic parasitic organism were it not for the experimental evidence in F_2, which precludes such a belief.

My warmest thanks are due Dr. E. M. East for suggestions and criticisms while engaged in this investigation.

July, 1912.

SHORTER ARTICLES AND DISCUSSION

HEREDITY IN A PARTHENOGENETIC INSECT (APHIS)[1]

Statement of Problem

As is well known, Johanssen has found that in self-fertilizing strains of beans selection within the strain—selection in the "pure line"—does not change the mean of successive fraternities. If this conclusion holds generally we should expect it to hold among parthenogenetic species also. Among asexually reproducing animals Jennings (1909) finds that it is true for *Paramecium* and Hanel (1907) for *Hydra*.

Shull (1910) has found that strains of *Hydatina* from New York differ from a strain from Baltimore in the rate of production of males, and Whitney (1912) has found a similar difference in strains. For *Daphnia* (Woltereck, 1910) the persistence of the mode is less easily determined because of a high degree of variability depending on conditions.

Insects seemed to offer a new field for such studies, one in which we might expect external conditions to play a smaller rôle, and because of the well-known parthenogenesis of Aphids and their availability it was determined to test so far as it could be done in a few weeks of a summer, the suitability of plant lice for studies of this sort.

Material and Method

After some experimenting it was decided to use *Aphis rumicis*, an aphid that commonly infests the poppies and nasturtiums about Cold Spring Harbor.

Potted poppies and nasturtiums were kept growing in the laboratory in large aquarium jars (about $\frac{1}{2}$ meter high) covered with cheese cloth. Each plant was carefully inspected to make sure that there were no aphids upon it. Then one gravid female was placed on each plant and its movements and reproduction carefully watched. All young in these summer broods were produced parthenogenetically.

[1] From The Biological Laboratory of the Brooklyn Institute of Arts and Sciences, Cold Spring Harbor, Long Island.

Brood No.	Mother				Offspring								
	Length		Ratio	Wings	1 12			2 13			3 14		
	3d Jt.	4th Jt.	3÷4		3d Jt.	4th Jt.	Ratio	3d Jt.	4th Jt.	Ratio	3d Jt.	4th Jt.	Ratio
1..	37	24	1.54	Absent	42	30	1.40	43	30	1.43	37	25	1.48
2..	37	23	1.61	Absent	42	29	1.45	45	26	1.73	46	30	1.53
					46	32	1.44	45	29	1.55	43	31	1.39
3..	—	—	—		38	25	1.52	38	26	1.46	37	26	1.42
4..	32	21	1.52	Absent	37	25	1.48	35	25	1.40	37	26	1.42
					39	29.5	1.32	39	29	1.34	41	30	1.37
5..	—	—	—		42	27	1.56	39	27	1.44	41	26	1.58
					41	24	1.71	41	27	1.52	39	29.5	1.53
5*a*.	35	24	1.46	Absent	29	19	1.53	28	18.5	1.51	26	17.5	1.49
					33	23.5	1.40	28.5	18.5	1.54			
5*b*.	33	27	1.22	Present	33.5	22.5	1.49	29	21	1.38	30	19	1.58
5*c*.	35	26.5	1.32	Present	24	15.5	1.55	23.5	15	1.57	28	16.5	1.70
6..	30	20	1.50	Absent	39	24	1.63	37	25	1.48	39	24	1.63
					34.5	24	1.44	37	26	1.42	32	22.5	1.42

Brood No.	Mother				Offspring								
	Length		Ratio	Wings	7 18			8 19			9 20		
	3d Jt.	4th Jt.	3÷4		3d Jt.	4th Jt.	Ratio	3d Jt.	4th Jt.	Ratio	3d Jt.	4th Jt.	Ratio
1..	37	24	1.54	Absent	41	27.5	1.49	37.5	27	1.39	38	22.5	1.69
2..	37	23	1.61	Absent	43	28.5	1.51	44	32	1.38	44	30.5	1.44
3..	—	—	—		35	24.5	1.43	33	23	1.43	36	26	1.38
4..	32	21	1.52	Absent	38	26	1.46	38	29	1.31	37	26	1.42
					35	25.5	1.37	35	24.5	1.43			
5..	—	—	—		40	27	1.48	39	25	1.56	36	25	1.44
					39	25	1.56						
5*a*.	35	24	1.46	Absent	27	18	1.50	29.3	19.5	1.50	30.5	20.5	1.49
5*b*.	33	27	1.22	Present	36	24	1.50	28	21.5	1.30	30	19	1.58
5*c*.	35	26.5	1.32	Present	26	16.5	1.58	27	17	1.59			
6..	30	20	1.50	Absent	31	22	1.41	36	27	1.33	35.5	26	1.37
					37	25	1.48	35.5	23	1.54	35	23	1.52

Offspring										
3d Jt.	4 15 4th Jt.	Ratio	3d Jt.	5 16 4th Jt.	Ratio	3d Jt.	6 17 4th Jt.	Ratio	Wings of These Offspring	Host Plant
41	24	1.71	41	27	1.52	40	25	1.60	Present	Shirley poppy (grew poorly)
43	30	1.43	44	29	1.52	44	30	1.47	Present	Opium poppy
44.5	33.5	1.33	42	29	1.45				(Winged)	
37	24	1.54	36	25.5	1.41	34	23	1.48	Absent (Wingless)	Shirley poppy
42	27	1.56	36	28	1.29	40	29	1.38	Absent	Nasturtium
40.5	29.5	1.37	36	26.5	1.36	36	26	1.38	(Wingless)	
45.5	28	1.63	40	27	1.48	39	26	1.50	Absent	Opium poppy
36	25	1.44	35	26	1.35	36	22.5	1.60	(Wingless)	
27	19	1.42	32	20	1.60	27.5	20	1.38	Absent (Wingless)	Opium poppy
20	16	1.25	31.5	20	1.58	32	23	1.39	Absent	Opium poppy
34.5	21	1.64	33.5	20	1.68	25	16	1.56	Absent	Opium poppy
35	23	1.52	36	24	1.50	36	25	1.44	Present	Opium poppy
35	22	1.59	37	24	1.54	38	26	1.46	(Winged)	

Offspring								
3d Jt.	10 21 4th Jt.	Ratio	3d Jt.	11 22 4th Jt.	Ratio		Wings of These Offspring	Host Plant
42	25	1.68					Present	Shirley poppy (grew poorly)
42.5	31	1.37	42.5	31	1.37		Present	Opium poppy
							Absent	Shirley poppy
38	27	1.41	39	30	1.30		Absent	Nasturtium
41	25	1.64	41	28	1.46		Absent	Opium poppy
29	18.5	1.57	28.5	20	1.43		Absent	Opium poppy
32.3	21.5	1.50	36	22	1.64		Absent	Opium poppy
							Absent	Opium poppy
35.5	22.5	1.58	36	23.5	1.53		Present	Opium poppy
36.5	22.5	1.62	36	24	1.50			

The characteristic whose inheritance it was finally decided to study was the ratio of the third antennal joint to the fourth antennal joint. This ratio offered the advantage of a fairly large range, *i. e.*, from 1.25 to 1.75; and the mode of a fraternity was soon observed to vary from about 1.35 to 1.55.

The measurements were made upon the mother at the same time with the offspring. The offspring were measured when it was obvious that they were mature and soon to breed. The insects were first etherized and the measurements were then made with a micrometer eyepiece, with a magnification such that the third antennal joint averaged about 32 units.

RESULTS

The following table gives the numerical data derived from the measurements made:

The ratios that are derived from measurements of the offspring are grouped into classes, and the frequency of the classes shown graphically in Figs. 1–7.

First, it appears that all aphids fall into two classes, winged and wingless. While the winged mothers had a smaller antennal ratio than the wingless mothers, the antennal ratio shows practically no difference in the winged and wingless *offspring*. Thus 10-winged offspring of a wingless mother give an average antennal index of 1.54, and 5 wingless offspring of the same mother give an average antennal index of 1.48. From a wingless mother with antennal index of 1.46 were derived 13 *wingless* offspring with an average index of 1.49, while from another wingless mother with antennal index of 1.50 were derived 22 *winged* offspring with an antennal index of 1.49. We may compare the antennal indices of the two lots of offspring whether they happen to be winged or not.

The nature of the food plant may be, on the other hand, of importance for the antennal index. Thus of two mothers with practically the same antennal index, one was fed on opium and the other on nasturtium. The progeny of the first finds its mode at 1.50 to 1.59; of the second at 1.30–1.39. It was not possible to determine from comparative studies whether there is uniformly a reduction of the index in the offspring of nasturtium-fed mothers, or whether this result was due to the fact that the nasturtium-fed mothers belonged to a special strain with a low index. In our ignorance it is clearly permissible to

compare only offspring from similarly fed mothers. All data considered below are from offspring of opium-fed mothers.

To decide whether or not we have "pure lines" in *Aphis* it is necessary to breed two generations of offspring; it is better

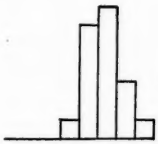


FIG. 1.
5
Opium poppy

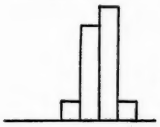


FIG. 2.
5a
Opium
Mother, 1.46.

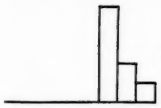


FIG. 3.
5c
Mother, 1.32.
Opium

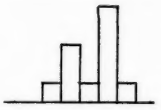
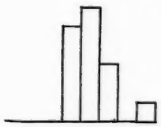


FIG. 4.
5b
Opium



Mother, 1.22.
FIG. 5.
2
Opium
Mother, 1.61

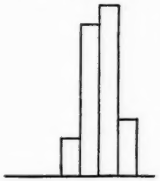


FIG. 6.
6
Opium
Mother, 1.50

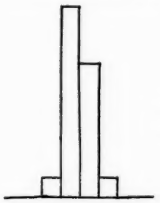


FIG. 7.
4
Nasturtium
Mother, 1.52

to breed more. It is necessary to breed two lines through these generations; it is better to breed three or more. The results so far obtained are inadequate since they continue only one line through two generations of offspring. The data obtained are as follows:

A wingless mother, whose antennal index was not obtained, was fed on opium poppy and produced 18 offspring. The distribution of the antennal ratios of these offspring is as given in Fig. 1. The mode is at 1.50–1.59, the average is 1.53. From this fraternity three individuals were now selected as mothers of the next. We may call them 5*a*, 5*b* and 5*c* (Figs. 4, 5, 6). 5*a* has the highest antennal ratio, 1.46. The mode of the progeny is at 1.55 (1.50–1.59) and the average ratio is 1.49. 5*c* has the next lowest ratio, 1.32. Her progeny also have the mode at 1.50–1.59. The third mother (5*b*) has a ratio of 1.22. The progeny is few in numbers and has two modes of which the major is at 1.50–1.59 like the two others; and the average is 1.47.

The foregoing series of facts may be tabulated as in Table *A*.

TABLE *A*

Family	Maternal Ratio	Offspring	
		Mode	Mean
5*a*	1.46	1.50–1.59	1.49
5*c*	1.32	1.50–1.59	1.61
5*b*	1.22	1.50–1.59	1.47

The table shows clearly that while the range in the maternal ratio is .24, the range in the means is only .14 and that there is no close relation between the order of the maternal ratios and the order of the fraternal means. In all the fraternities the mode stands in the 1.50–1.59 class.

CONCLUSIONS

In so far as this series goes, then, it speaks for the conclusion that, in the parthenogenetic *Aphis rumicis*, the progeny does not inherit the somatic idiosyncrasies of the parent but does inherit from the underlying germ plasm common to all; and hence progeny of somatically quite different sisters tend, on the average, to be alike. The somatic differences in the parthenogenetic line are not inherited.

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THE HIMALAYAN RABBIT CASE, WITH SOME CONSIDERATIONS ON MULTIPLE ALLELOMORPHS

IT has been shown by Castle ('06, '09), Hurst ('06) and Punnett ('12) that the Himalayan pattern in rabbits behaves as a simple recessive to self color, and as a simple dominant to albino. Thus, as Punnett points out, we might suppose self to be the double dominant, Himalayan a recessive in one factor, and albino a double recessive. But, to use Punnett's words:

The F_2 from self $\times$ albino should consequently contain Himalayans as well as true albinos. But among the large number of animals reared from such matings no Himalayans have hitherto been recorded, and for the present the relations between these various forms remain obscure.

If we suppose that albino may be either the second single recessive or the double recessive we avoid this difficulty, but are then unable to explain why albino $\times$ Himalayan should not, at least occasionally, produce selfs by recombination.

Now it seems to me that the facts of the case are fitted equally well by either of two hypotheses. In the first place, we may consider, as above, that Himalayan is a single recessive and albino a double recessive—if we suppose the two factors concerned to be completely linked. The gametic (not zygotic) constitution of the three types would then be represented thus, C being the color producer and S the factor changing Himalayan to self.

Self — CS
Himalayan — Cs
Albino — cs

If C and S be completely linked no cS individual can be obtained, and $CS \times cs$ would give no Cs in F_2.

On the other hand, we may consider the factor for self as allelomorphic to that for Himalayan pattern, and also to that for albinism. Then the three pure types might be represented thus (zygotic formulæ):

Self — SS
Himalayan — HH
Albino — AA

S, H, and A being allelomorphic each to itself or to either of the others, the crosses would result thus:

Self — SS
Himalayan — HH

F_1	SH — self
F_2	SS, SH, SH — 3 self; HH — 1 Himalayan

Self — SS
Albino — AA

F_1	SA — self
F_2	SS, SA, SA — 3 self; AA — 1 albino

Himalayan	— *HH*
Albino	— *AA*
F_1	*HA* — Himalayan
F_2	*HH*, *HA*, *HA* — 3 Himalayan
	AA — 1 albino

An explanation similar to the second one above has been given by de Meijere ('10) for Jacobson's results with *Papilio Memnon*. The evidence on this case is, however, very incomplete, and there are complications due to sex. Either triple allelomorphs or complete coupling would seem to cover the facts as we have them at present. Shull ('11) has also used a system of three allelomorphs for a case in *Lychnis dioica*. I shall refer to this case again.

It will be seen that triple allelomorphs may be substituted for complete coupling as an explanation of any case where only three of the four combinations possible on the complete coupling scheme are known. But if we have the double dominant, both single recessives, and the double recessive, then triple allelomorphism will no longer work. Thus, if a race of albino rabbits is discovered which produces self when mated to Himalayan, complete linkage will be the most likely explanation of the case.

There are certain other cases which fulfil the above requirements. Emerson ('11) has reported a case in beans (green leaves—green pods, green leaves—yellow pods, and yellow leaves—yellow pods are the three races concerned). The similar cases of complete linkage reported for corn by East and by Emerson are probably more easily explainable by linkage than by multiple allelomorphs, as, at least in some cases, all four possible races are found. Baur ('12) has a case in *Aquilegia*, where three types of leaves are found—green, variegated (green and yellowish green), and yellowish green. These behave toward each other in a manner exactly similar to that of the self, Himalayan and albino rabbits. Finally, Morgan ('12) has reported a case in *Drosophila ampelophila*. Red eye is a dominant to eosin and to white, and eosin is also a dominant to white. No two types ever give the third when crossed, either in F_1 or in F_2. The explanation which has been given in beans, columbines and flies has been that of two allelomorphic pairs, completely linked to each other.

The question as to which of these views is the more probable is closely bound up with the presence and absence hypothesis. On a strict application of this idea there is of course no possibility of more than two members of any given allelomorphic group. The presence and absence hypothesis as a universal principle has been criticized by Morgan ('13) in a recent paper, on what seem to me very strong grounds. It seems very unlikely that protoplasm (chromatin?) is such a simple substance that the only possible change in a given unit (molecule?) involves the loss of that unit. On the other hand, if a slight change takes place in a chemically complex gene, is it necessary to suppose that its allelomorphic relations must be upset? That very slight changes in the constitution of a gene might easily affect its behavior in ontogeny will, I think, be readily granted.

It is to be noted that in all the cases cited above the supposed three allelomorphs have similar ontogenetic effects. Thus the three in rabbits, in *Aquilegia,* and in *Papilio* all affect the distribution of pigment (and, in *Papilio,* also the shape of the wings), those in *Lychnis* the sex, those in beans the production of the same color in different organs, and those in *Drosophila* the production of different colors in the same organ. This may perhaps seem to be in favor of the view that we have here different modifications of the same gene, rather than two distinct genes and their absences.

The history of the red-white-eosin group of eye colors in *Drosophila* is interesting when considered from the viewpoint of the presence and absence hypothesis. The first white-eyed fly arose as a mutant in red stock. On presence and absence it must have been caused by the simultaneous loss of two factors, which were called *C* and *O* by Morgan. Then, in white-eyed stock there appeared an eosin-eyed fly. Here the factor called *O,* just lost, must have been put back again. Finally, in one of my own cultures, eosin has given rise to white by mutation.[1] In both these latter cases the flies had miniature wings, and in the white-to-eosin case they also had black body color. These characters give a check on the results, and make it extremely unlikely that any contamination had occurred. Further evidence to this effect is

[1] After this paper went to press it was pointed out to me by Mr. H. J. Muller that there is another possible explanation of this case, which does not involve mutation from eosin to white. This interpretation can not be entered into until certain phenomena observed by Mr. C. B. Bridges have been more fully investigated.

given, in the eosin-to-white case, by the fact that the mutant fly was one of 127 obtained from a single pair, all of her brothers and sisters being of the expected classes (half of the females heterozygous for white), as were likewise the flies from six sister pairs.[2]

The presence and absence hypothesis involving a dropping out of whole genes or addition of entirely new ones does not offer as simple an explanation of this case as does the conception that we have here a relatively unstable gene, which does not drop out entirely, but undergoes various changes, that from white to eosin being reversible.

It should be noted that Shull ('11) has reported a case of what he calls reversible mutation in the sex-determining factor in *Lychnis*, which is very similar to the above red-eosin-white case. He has adopted a system of triple allelomorphs to explain it, though admitting that complete linkage will also cover the facts. He has also considered the bearing of the case upon the presence and absence hypothesis and upon the nature of mutation, reaching conclusions somewhat similar to those given above.

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MENDELISM AND INTERSPECIFIC HYBRIDS

THE complications of modern Mendelism have greatly increased the difficulty of discussing the practical applications of heredity. The word Mendelism itself has two essentially different meanings that are being used indiscriminately. A particular form of alternative inheritance is called Mendelism and the same name is applied to a general theory of heredity. It is true that the Mendelian theory was suggested by the Mendelian form of inheritance, but the facts are also capable of other interpretations. Many of the proposed applications of Mendelism to breeding and eugenics are in reality only inferences from the theory and are not in real accord with the facts on which they are supposed to be based.

An example of such a discrepancy may be found in the AMERICAN NATURALIST for July, 1912, in a paper entitled: "Evidence of Alternative Inheritance in the F_2 Generation from Crosses of *Bos indicus* on *Bos taurus*." Though readers are evidently expected to believe that the hybrids are showing a typical Mendelian inheritance of the contrasted parental characters, the facts stated in the paper show that the behavior of the hybrids is not in accord with the Mendelian theory of heredity. Alternative inheritance is manifested in these bovine hybrids, but it is not the Mendelian form of alternative inheritance, with the contrasted parental characters behaving as independent units combined by the laws of chance. Instead of showing a Mendelian freedom of combination of the contrasted characters, these hybrids afford a much better illustration of a different principle of heredity, the coherence of characters derived from the same parental stock.

As the paper by Dr. Nabours seems to represent the only attempt that has been made to give a scientific account of a unique series of hybrids, it would be very undesirable to have the general conclusion regarding the application of Mendelism accepted without challenge. In addition to the scientific questions involved, the importance of finding the best way of securing a full utilization of the tick-resistant Brahma cattle in Texas will appeal to all who have had the pleasure of seeing Mr. Borden's imported animals and their hybrid offspring. But practical recommendations are hardly in order until the facts are better under-

stood. To view these hybrids as a typical case of Mendelism is to overlook some of the distinctions which need to be recognized before correct applications can be expected.

ALTERNATIVE INHERITANCE

It seems to be taken for granted by Dr. Nabours, as by many other recent writers, that all forms of alternative inheritance represent the so-called Mendelian principle of heredity, that is, the alternative transmission of unit-characters in pure germ-cells. In reality the facts of alternative inheritance extend far beyond the field of Mendelism into regions where the Mendelian conception of alternative transmission can not be applied.[1]

The old assumption regarding hybrids and mixed races was that they represented intermediate combinations or averages between the contrasted characters of the parental stocks. A generation ago belief in "the swamping effects of intercrossing" was even more general among biologists than acceptance of Mendelism is now. But we have learned that the "swamping effects" were largely imaginary. The scientific world has its history of easily forgotten fads, no less than the world of politics or fashion.

The usual result of crossing is not the formation of an intermediate average, but the reappearance of the parental characters in the later generations of the hybrids, if not in the first. Recognition of the principle of alternative inheritance is having a revolutionary effect upon the science of heredity. The facts of Mendelism are of special interest because they represent extreme cases of alternative inheritance, but the interest is in no way dependent upon the Mendelian theory of heredity. Indeed, the theory often interferes with appreciation of the facts.

MENDELISM A THEORY OF ALTERNATIVE TRANSMISSION

Mendelism, as a theory of heredity, is an assumption that alternative inheritance is due to alternative transmission of independent particles or "units," which are supposed to represent the characters in the protoplasm at the time when the germ-cells are formed. If sufficient magnification could be applied, so that the structure of the protoplasm in the germ-cells could be fully

[1] Cook, O. F., "Dimorphic Leaves of Cotton and Allied Plants in Relation to Heredity," Bulletin 221, Bureau of Plant Industry, U. S. Department of Agriculture, pp. 36–50.

shown, believers in the Mendelian theory would expect to find separate "gens" or discrete particles of some sort to represent the various characters of the adult animals or plants. The gens that represent the characters of different parents are supposed to remain entirely distinct and to find their ways into different germ-cells. Each germ-cell of a hybrid is supposed to receive only a single set of these hypothetical character-units or gens, representing the contrasted characters of the parents, and the sets are supposed to be made up by chance assortment. Thus the different germ-cells produced by a hybrid are supposed to represent all the combinations of the contrasted parental characters that are theoretically possible under the laws of chance.

The theory of Mendelism has greatly stimulated the study of cytology, in the hope of finding the supposed character-germs as actual, visible particles in the protoplasm. Some writers have argued that the chromosomes or chromomeres represent the characters, or at least the contrasted Mendelian characters, and have attempted to trace a definite relation between the behavior of the chromosomes and the inheritance of the characters. Other writers do not indulge in such speculations, but believe in alternative transmission for mathematical reasons. Typical cases of Mendelism are relied upon as affording sufficient proof of the theory of alternative transmission. The Mendelian theory accords with the numerical facts of Mendelism, but this is not a sufficient proof of its correctness, for it is not the only interpretation that the facts will admit. Elaborate Mendelian computations create in the casual reader an impression of mathematical certainty, but the same computations could be made under other theories of alternative inheritance.

Alternative Inheritance and Normal Diversity

The facts of alternative inheritance are not at all confined to cases where the characters show the exact numerical proportions typical of Mendelism. Alternative inheritance is a general law that applies even in the vast and highly diversified groups of interbreeding individuals that constitute natural species. The typical Mendelian cases usually appear as results of previous artificial breeding of pure strains.[2]

The normal diversity (heterism) everywhere manifested among

[2] Cook, O. F., "Pure Strains as Artifacts of Breeding," The American Naturalist, 43: 241, April, 1909.

the members of natural species is a result of alternative inheritance of contrasted parental characters, no less than the typical cases of Mendelism. If inheritance were not alternative, heterism would not be maintained. Each species or separate group of interbreeding individuals would gradually decline into a general uniform average. Under conditions of normal interbreeding among the representatives of different lines of descent there is no such tendency to uniformity. The offspring of the same parents differ normally among themselves in the same ways that the parents and ancestors have differed. Though each individual can bring into expression only one set of differences, other ancestral characters are likely to reappear in later generations. It is only by special methods of breeding in single or narrow lines of descent that conditions of uniform heredity can be established.

ALTERNATIVE EXPRESSION INSTEAD OF ALTERNATIVE TRANSMISSION

That characters are transmitted without being brought into expression is one of the best known facts of heredity, for which the theory of Mendelism makes no adequate provision. The idea of alternative expression of characters accommodates the numerical data of Mendelism as well as the idea of alternative transmission, and is in far better accord with other facts of variation. Diversity in natural species, and reversions that arise in select varieties and in hybrid stocks, afford adequate evidence for holding that alternative inheritance is due, not to alternative transmission of characters, but to alternative expression. When the facts of alternative expression are taken into account the theory of alternative transmission becomes unnecessary.[3]

COHERENCE OF CHARACTERS IN INTERSPECIFIC HYBRIDS

The contrasted characters of interspecific hybrids do not behave as independent Mendelian units, but tend to remain more or less united with others derived from the same parental stock. This coherence of expression often interferes with the formation of the combinations of characters according to the Mendelian theory of independent segregation of discrete units.[4]

[3] Cook, O. F., "Transmission Inheritance Distinct from Expression Inheritance," *Science*, N. S., 25: 911, 1907.

[4] Examples of coherence of characters in cotton hybrids have been de-

Mendelian reactions are likely to be obtained when defective mutations, such as cluster cottons or hornless breeds of cattle, are crossed with normal varieties, but not when normal representatives of two species are crossed, like the Upland and Egyptian cotton or the cow and the zebu. Though there can be no question of the purity of the parental stocks with reference to many contrasted characters, interspecific hybrids seldom show the typical Mendelian behavior.

Non-Mendelian Behavior of the Bovine Hybrids

The facts stated by Dr. Nabours regarding the bovine hybrids do not show that the behavior of the characters is essentially Mendelian. Even if the parental breeds were segregated in the same proportions as in simple Mendelian hybrids, the result would still be essentially non-Mendelian, for the parental types differ by many sharply contrasted characters. Such a segregation of "pure Brahma and pure Durham" would mean that there had been a complete coherence of all of the characters of the two parental stocks, instead of a Mendelian segregation and recombination of independent units. The actual facts appear to lie somewhere between complete coherence and complete segregation.

If the Mendelian conceptions of heredity applied to these bovine hybrids, the segregation of "pure Brahma and pure Durham," instead of appearing to be the rule, would occur only in extremely rare cases, because of the numerous differences of the parental types. Indeed, my own impression on this point is somewhat more Mendelian than the account given by Dr. Nabours. Though it was noticed that several individuals of the second generation were distinctly more Brahma-like and more Durham-like than any of the first generation, there were only two or three that suggested the idea of complete segregation of the parental types. The fact that impressed me was not that so much segregation of the contrasted parental characters had taken place in the second generation, but so little. The various colors and textures of hair and skin, the horns, humps and dewlaps were generally brought into coordinated, harmonious expression,

scribed in several publications of the Bureau of Plant Industry, U. S. Department of Agriculture. Bull. 147, "Suppressed and Intensified Characters in Cotton Hybrids"; Bull. 156, "A Study of Diversity in Egyptian Cotton," and Cir. 66, "Cotton Selection on the Farm by the Characters of the Stalks, Leaves and Bolls."

instead of behaving as separate "units" combined by indiscriminate alternative transmission. Even the more complete reversions to the parental types may be considered as results of non-Mendelian coherence of characters in expression, rather than as examples of Mendelian segregation and recombination of independent "units."[5]

COMPARISON OF BOVINE HYBRIDS WITH COTTON HYBRIDS

The practical question to be determined is whether the Durham-like and Brahma-like individuals of the second and later generations are equal to the original parental varieties, and whether the intermediate individuals maintain the average of the first generation. In the second generation of interspecific cotton hybrids it is usual to find many degenerate plants with an obvious resemblance to one or the other of the parental stocks, though usually abnormal and inferior. But among the cattle the second generation hybrids seemed much less different from the first generation, both in constitution and in external features. No general tendency to inferiority in the second generation, as compared with the first, either in vigor or in resistance to ticks, had been detected by Mr. Borden. But the experiments have not continued long enough to afford adequate evidence on this point.

If the analogy of cotton should be found to apply with the bovine hybrids the Brahma-like and Durham-like animals that appear in the second and later generations will not prove to be equal to the Brahmas and Durhams that have not been hybridized, nor will the intermediate individuals show as high an average as the first generation. One of the usual results of crossing, even among varieties of the same species, is to destroy the effects of previous selection in establishing a uniform expression of the characters of the parent varieties. The fact that many of the second generation of Brahma hybrids are magnificent animals does not prove that equally superior hybrid varieties can be established. To increase the pure stock of Brahma cattle, and thus increase the possibilities of producing first generation hy-

[5] In a more recent paper Dr. Nabours has recognized the divergence from typical Mendelism, in the following statement: "As a matter of fact, observations made this summer and to be described later, indicate that the segregation is not so simple as it at first appeared to be." See, "Possibilities of a New Breed of Cattle for the South", in American Breeders Magazine, **4**: 45, March, 1913.

brids, may be more important than the breeding of hybrid varieties. At least this is the suggestion to be drawn from the failure of many attempts to develop superior useful varieties of cotton and other seed-propagated plants from interspecific hybrids. As a barrier to a permanent union of two species degeneration in the second or later generations of a hybrid stock may be as effective as sterility in the first generation. It may prove very fortunate that Mr. Borden has imported Brahma cows as well as bulls, for this may make it possible to perpetuate the Indian breeds in Texas.

A tendency to deterioration in the later generations of hybrids is likely to be masked as long as hybrids are crossed back on one of the parental stocks, instead of being bred with each other. This is because even dilute hybrids share some of the stimulation effect shown in the first generation. But these questions of vigor and fertility, though of fundamental importance in practical breeding, lie outside of the range of the Mendelian theory. Vigor and fertility are phenomena of expression in the first generation, whereas the theory of Mendelism relates to the transmission of characters to the second and later generations. Mendelism has served a useful purpose in opening the way to a better understanding of the various forms of alternative inheritance, but the overshadowing Mendelian theory of heredity as a process of alternative transmission of character-unit particles needs to be cleared away.

This theory that alternative inheritance is due to alternative transmission does not lead to more correct ideas of the nature of heredity or to better methods of breeding. Instead of providing us with a simple method of making any desired combination of characters of different species, as writers on Mendelism have led the public to believe, the facts of alternative inheritance indicate that it is very difficult, if not altogether impossible, to secure permanent combinations of characters of different species. In plants that can be propagated from cuttings, hybrid combinations can be maintained, but this affords no assurance regarding types that are limited to sexual reproduction.

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December 27, 1912

ORDOVICIAN (?) FISH REMAINS IN COLORADO

DURING the past year Mr. P. G. Worcester, of the Colorado Geological Survey, has been investigating certain strata near Ohio City, Colorado, supposed to be of Ordovician age. The particular horizon under discussion contains *Receptaculites oweni* Hall (southeast of Fairview Mt.), *Halysites catenulatus* (L.) (basin east of north end of Fossil Ridge), *Platystrophia* (?) sp. (Fossil Ridge), and *Heliolites* (?) sp. with *Halysites catenulatus* at head of Alder Creek, west of Fossil Ridge. The *Heliolites* (?) is the same as that in the Cañon City Ordovician. These fossils were identified by Professor J. Henderson, and so far as it is possible to determine from them, the rocks should certainly be Ordovician. The first Devonian fossils were found about 100 feet above this horizon.

However, closely associated with the invertebrates cited, and certainly of the same age, are rather numerous fragmentary remains of fishes. These may be briefly described as follows:

1. A fragment of a plate exhibiting fine grooves with deep pits; resembling, so far as it goes, the plate of *Coccosteus disjectus* from the Old Red Sandstone, figured by A. S. Woodward, Cat. Fossil Fishes Brit. Mus., Part II, pl. VIII, fig. 1. The structure is also nearly identical with that of *Astraspis desiderata*, from the Ordovician of Cañon City, as figured by Walcott, Bull. Geol. Soc. Amer., Vol. 3 (1891), pl. 3, f. 7. Some of the other figures of *Astraspis* might well belong to Coccostean fishes.

2. A large fragment, having a diameter of over 30 mm., is covered with irregular obtuse vermiform ridges, and is *exactly* like the opercular plate of *Rhizodus ornatus* (Woodward, t. c., pl. xii, f. 5). so far as the sculpture goes. This particular species is lower Carboniferous, but Rhizodontid fishes also occur in the Devonian.

3. Numerous fragments of striated spines, some short, conical and straight; others more slender and curved. These appear to exactly correspond, so far as they go, with the spines of *Diplacanthus*, from the lower Old Red Sandstone. One of the supposedly Coccosteoid plates, 5 mm. thick, with the surface finely striate, with punctate more or less branching striæ or grooves, occurs in the same piece of rock as a supposed *Diplacanthus* spine, the two almost touching.

According to the available evidence, we seem therefore to

have three families of fishes represented: (1) Coccosteidæ; (2) Rhizodontidæ; (3) Diplacanthidæ. The genera and species can not be precisely determined.

These fish remains, taken by themselves, would certainly be regarded as Devonian. Walcott's Ordovician species from Cañon City were said by Professor James Hall to have such a Devonian facies that he would certainly have referred them to the Devonian, but for the accompanying invertebrate fauna.

In general, when there is a conflict between the evidence from vertebrate and invertebrate fossils, the vertebrates must be allowed the most weight; but it is evident that the numerous and varied Devonian fishes had ancestors, so it is to be expected that types more or less like those of the Devonian will be found in older rocks. I understand from Mr. Worcester that there is no reason to believe that the Silurian is represented in the locality.

Schuchert ("Paleogeography of North America") remarks that in the Ordovicic or Ordovician, during the retreat of the sea,

> The first evidence of those peculiar heavily armored fishes belonging to the ostracoderms appears in cleanly washed beach sands and less abundantly in dolomites at three widely separated places in Colorado and Wyoming. They are now all fragmentary and seem to have been washed into the sea by the rivers. From this can it be inferred that during some earlier inundation the marine ancestors of these fishes were retained upon the land in relict seas, and under the stress of evanescent waters became modified into the armored double-breathing animals that gave rise later to the true fishes? Such being the interpretation, the marine fishes must then have been derived from land [freshwater] fishes, as suggested by Chamberlin and Salisbury.

The two localities in addition to the famous one at Cañon City are (Dr. Eastman in litt.) in the Big Horn Mts., and in the Black Hills uplift, in a bed lying above the Deadwood Formation. Both were discovered by Mr. N. H. Darton. These all agree in the character of their fish remains.

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December 14

NOTES AND LITERATURE

SOME RECENT ADVANCES IN VERTEBRATE PALEONTOLOGY. II.

Waldemar Lindgren in a discussion of "The Tertiary Gravels of the Sierra Nevada of California,"[11] gives (p. 51) a brief review of the history of fossil mammals of the auriferous gravels of California. In this connection the author has touched on the age of the famous "Calaveras skull," which some have thought indicated a Tertiary age for man in California. The skull has in the past provoked much discussion and it is interesting to have new light brought forward. Mr. Lindgren, through his associate, Mr. J. M. Boutwell, interviewed some of the older residents of the region in which the "Calaveras skull" was found. One resident remembered the details of the "find" and stated to Mr. Boutwell that the mine in which the skull was found had been "salted" with the subsequently famous "Calaveras skull" as a practical joke by one of the neighborhood humorists. While this is not of very definite evidence for the non-Tertiary age of the "Calaveras skull" yet it fully sustains the important researches of Sinclair and Holmes, who could find no good evidence for the skull being other than that of the modern Indian.

The *Kansas University Science Bulletin* issued during the past summer contains three articles on fossil vertebrates. A new species of *Eryops* (*E. willistoni*) and the history of the development of our knowledge of the temnospondylous Amphibia is the subject-matter of one of the papers. The earliest known temnospondyle was described by Agassiz as a fish in 1777. The amphibian nature of the fossil was not noted until 1847 when it was correctly defined by Goldfuss and later by Jaeger. A list of 58 species is given, nearly or quite all of which belong with the Temnospondylia. The order Temnospondylia and the family Eryopidæ are defined and the geological range and geographical distribution given. The new temnospondyle (*Eryops willistoni*) is from the reputed Permian of Oklahoma. The species is quite distinct and the characters are shown in six plates of drawings of the skeletal remains.

An armored Dinosaur (*Stegopelta landerensis* Williston) is

[11] Prof. Paper 73, U. S. Geol. Surv.

described in another paper[12] and illustrated in five plates. The material is in the University of Chicago. The form is one of the later, peculiar, armored, bizarre, stegosaurian dinosaurs allied to *Polacanthus* of England, *Stereocephalus* of Canada, *Hierosaurus* of Kansas Niobrara Cretaceous, *Ankylosaurus* of Montana and other widely distributed genera of armored dinosaurs. The dinosaur was found in a marine deposit associated with plesiosaur remains. A short sketch of the horizon, the Hailey shales of the Wyoming Cretaceous, is given.

The soft parts of Cretaceous fishes are described and figured in the other paper,[13] and a new herring from the Cretaceous near Waco, Texas, is described as *Thrissopater intestinalis*, so called on account of the preservation of the intestines. The form is allied to *T. magnus* of the English Cretaceous. Another form of fish, identified provisionally as *Empo nepaholica* Cope, is represented by the cast of the stomach, a portion of the intestine and a pectoral fin with a few scales.

Dr. S. W. Williston has reviewed the question of the homology of the *wing finger* of Pterodactyls[14] and has given a new restoration of a pterodactyl as it probably appeared in life. The restoration is based on Dr. Williston's previous restoration of the skeleton of *Nyctosaurus gracilis* Marsh published in Eastman's translation of Zittel's "Paleontology" (II, 255).

The question which has interested anatomists for nearly a century is whether the wing finger of the pterodactyls is the fourth or fifth. There have been many arguments for each determination. Cuvier was the first who correctly interpreted the homology of the wing finger, basing his determination on the phalangeal formula of other reptiles. Plieninger has recently raised the question as to whether the interpretation of the phalangeal formula, 2, 3, 4, 5, 3 for the hand and 2, 3, 4, 5, 4 for the foot, is the primitive one for the Reptilia. Dr. Williston answers this question conclusively in the affirmative and quotes as evidence newly acquired facts from the Permian vertebrates of Texas and New Mexico. To substantiate his claim he figures the entire arm of three genera of Permian reptiles, *Limnoscelis, Ophiacodon* and *Varanosaurus*. In all of these genera, known from nearly perfect material, the phalangeal formula is as given above.

The author gives further notes on the function of the pteroid

[12] Vol. V, No. 14.

[13] Vol. V, No. 15.

[14] *Journ. Geol.*, XIX, 696–705, 4 figs.

bone, which has been interpreted as a vestige of the first finger. He considers it to be simply an ossified tendon supporting the patagial membrane running from the arm to the neck. He bases this conclusion on the relations of this structure in the well preserved skeleton of *Nyctosaurus* in the Field Museum fully described some few years ago by Dr. Williston.

In view of these facts there seems no longer to be any question that the wing finger of the pterodactyls is the *fourth*. The reduction of the phalanges of the wing finger from the primitive number of 5 to 4 is accounted for on the assumption that the claw of the finger has been lost as has the same structure in the bats. Further evidence is brought forth in the nature of the carpus to sustain the homology of the wing finger of the pterodactyls with the fourth digit of other reptiles.

The *Annals of the Queensland Museum*[15] contains two articles on fossil vertebrates by C. W. de Wis, former director of the museum. One of the papers describes a new species of bird, *Palæolestes gorei*, based on a single phalange. The specimen is carefully described, but the geological position is not given, the comparisons of the new form with other species of the same kind are not attempted so that one wonders just why the paper was published, since it really throws no new light on the subject excepting perhaps to extreme ornithological experts.

The same author in a few lines describes a new cestraciont fish from a single imperfect tooth. The form is insufficiently defined and no comparisons are given.

A new member of the theropodous Dinosauria has been described by Mignon Talbot[16] from remains discovered in an "erratic bowlder" of Connecticut Valley Triassic sandstone, which according to Talbot was carried two or three miles from its original source by the glacier. The stone contains the larger part of the skeleton of a small dinosaur of the carnivorous type, a member, undoubtedly, of those reptiles which made the so-called "bird-tracks" in the Connecticut Valley sandstone, so admirably described by Hitchcock, Lull and others. The find is a very unusual and exceedingly interesting one, since Triassic dinosaurs are not at all abundant. The animal when alive could not have been much larger than an ordinary-sized chicken, thus serving to restrain the common conception of dinosaur sizes.

[15] Brisbane, Australia, No. 10, November, 1911.

[16] *Amer. Journ. Science*, June, 1911.

Portions of the hind limb, arm, skull, ribs, ventral scutellæ or abdominal ribs and portions of about thirty vertebræ are briefly described. The animal is compared with *Compsognathus*, to which it is closely allied and the new generic and specific terms, *Podokesaurus holyokensis*, are proposed. The specimen has been sent to Yale University Museum, where it will be prepared and further described by Dr. Lull.

Osborn[17] has given a discussion of the "Crania of *Tyrannosaurus* and *Allosaurus*," illustrated with many beautiful figures, photographs and drawings. The discussion of the osteology of the skulls is based on the most recent nomenclature of the cranial elements and the various specimens are figured from many points of view, so that the reader gets an adequate notion of the appearance of the skulls of these remarkable dinosaurs. The figures (Plates III and IV) of the brain cavity, which is figured from the dorsal side in Fig. 17, will be of great interest to the general zoologist.

Comparison of the intracranial cavity of *Tyrannosaurus* with the mid-section of the skull of *Sphenodon* and brain *in situ* as figured by Dendy shows that the intracranial cravity in *Tyrannosaurus* corresponds with the outer surface and foldings of the *dura mater* and is thus merely a cast of the outer envelope of the brain, which gives us little idea either of the form or size of the brain itself. . . . The cast of *Tyrannosaurus* gives us a means of measuring the size of the *dura mater* envelope. It displaces 530 cubic centimeters of water. If the brain proper bore the same proportion to the *dura mater* envelope as that of *Sphenodon*, the bulk of the brain of *Tyrannosaurus* may be estimated at 250 cubic centimeters.

This sized brain in a skull 50 inches in length would not indicate a high degree of intelligence.

Further on in Part II of the same memoir the same author discusses "Integument of the Iguanodont Dinosaur *Trachodon*," based on a marvelously complete "mummy" discovered in the Cretaceous of Converse County, Wyoming. The "mummy" and the impressions of the skin are figured in several excellent halftone plates, with explanatory line drawings. Osborn says of the skin:

Properly speaking the skin is not squamate, or imbricating, as in the lizards, but is rather tuberculate. There is no evidence of a squamous overlapping, or of an imbricating arrangement of the scales anywhere.

Although this bipedal dinosaur when standing erect attained a

[17] *Memoirs of the American Museum*, N. S., Vol. I, pt. 1, 1912.

height of 14 feet the individual tubercles are of very small size, never attaining a greater diameter than 5 millimeters. The paper closes with a reconstruction of *Trachodon mirabile* Cope in two attitudes, bipedal and quadrupedal and a discussion of a "Theory of Color Pattern" and "Habits of the Trachodonts." In regard to *Trachodon annectans* Osborn says:

> If the animals had spent any considerable part of their lives on dry land, even on the sands bordering the streams, the effect of the impact would certainly be observed in the retention of hoofs or ungues, in the coarsening of the palmar epidermis of the manus, because the fore limbs would certainly have been used occasionally, at least, in contact with the earth. There are no hoofs and the epidermal thickenings or pads are very lightly developed.

The conclusion then seems to be that the animals were largely aquatic.

The same author in Part III of the same series gives the attempts to arrive at some definite system of measurements for mammalian skulls with especial reference to the horse, in a paper entitled "Craniometery of the Equidæ." The author divides the discussion into (I) *Craniometric Systems, 1875–1912;* in which is given the results of the labors of Franck, 1875; Branco, 1883; Nehring, 1884; Tscherski, 1892; Salensky, 1902; Ewart, 1907; Bradley, 1907; and Osborn, 1912, the discussions being illustrated by figures and tables. (II) *Distinctions between Horses, Asses and Zebras.* (III) *Cytocephaly, the Bending of the Face on the Cranium,* the chief conclusions of which are: (1) in young animals the palatal and cranial lines are more nearly in the same plane; (2) in certain animals the deflection increases rapidly with age; (3) a horizontal and upward deflection is generally characteristic of primitive browsing types; (4) the downward deflection of the face and palate is highly characteristic of certain grazing types. (IV) *Craniometry and Odontometry in Paleontology.*

> In fossil skulls the *indices* lose value because the slightest degree of crushing or distortion seriously disturbs an index. Nevertheless the indices and ratios should be used wherever obtainable. Since fossil skulls and dental series are rarely complete or perfect, the paleontologist requires an additional series of detailed measurements of parts of the skull not needed by the zoologist.

Harold J. Cook in Volume 7, Parts 3, 4, and 5, of the Nebraska Geological Survey has given descriptions of a new genus and

two new species of Miocene rhinoceroses and a "Faunal Lists of the Tertiary Formations of Sioux County, Nebraska." These formations extend from the Lower Oligocene to the Pleistocene and many species are listed, 11 pages being taken up with the lists. Peterson,[18] however, states that one of the above species was based on a deciduous dentition.

Dr. R. S. Lull in the *Yale Alumni Weekly* of November 8, 1912, gives a very interesting account of his expedition to Texas in search of the remains of early horses, which he found in abundance.

Broili[19] has described very carefully a new specimen of *Pterodactylus micronyx* H. von Meyer from the lithographic slates of Eichstaedt in Bavaria. The nearly complete animal is seen from the dorsal side as it lies in the stone.

The same author[20] describes and figures very fully the osteology of the skull of *Placodus* based on a series of specimens of this peculiar, primitive, yet highly specialized reptile. On page 151 are given four reconstructions of the dorsal, ventral, lateral and occipital views of the skull. The animal is very peculiar in many ways and of very uncertain relationship, being assigned to several reptilian groups by the various authors who have studied the species. The maxillary and palatine teeth have the unusual form of pavement crushing teeth, the palatine teeth are especially large and broad, the middle one of the three on each palatine measuring nearly one by two inches. That the animal was a feeder on molluscs or hard vegetation would seem quite probable. Zittel in his "Handbuch der Paleontologie" lists six species of this genus; the one described by Broili being *P. gigas* Ag. The animal possesses a single temporal opening in the skull and amphiplatyan vertebræ, with the nostrils located far back on the skull with the nasals reduced, indicating an aquatic habit of life.

In the *American Journal of Science* for November, 1912, S. W. Williston describes and figures further portions of the osteology of the peculiar Permian reptile *Limnoscelis* from New Mexico, together with a restoration of the skeleton of the species *L. paludis* Will. Nearly the entire osteology of the species is

[18] *Science*, December 6, 1912, p. 801.

[19] *Zeitschrift der Deutschen Geologischen Gesellschaft*, Bd. 64, Jahrg. 1912, H. 3.

[20] Paleontographica, Bd. LIX, pp. 149–155, with figures and Taf. XIV.

known and much of it is preserved intact. Only a few caudal vertebræ and a few spines of the vertebræ are unknown, which for a fossil form is remarkable. In regard to the habits of the animal the author says:

> Taking into consideration the very short and stout legs with their broad flattened feet, the absence of claws, the elongate body and tail, it would seem not at all improbable that *Limnoscelis* was more or less at home in the water, though not strictly an aquatic animal. In much probability it lived in and about the marshes on the mud flats. . . .

From the press of the E. Schweizerbart'sche Verlagsbuchhandlung Nägle und Dr. Sprösser, Stuttgart, 1912, is a volume entitled "Grundzüge der Paleobiologie der Wirbelthiere," von O. Abel, professor of paleontology in the University of Vienna. The work comprises an octavo volume of 708 pages with 470 figures and a photographic reproduction of the skeleton of *Cryptocleidus oxoniensis* Phil. as mounted in the American Museum. The work is dedicated to Louis Dollo, professor of paleontology in Brussels. The work is divided into four sections as follows: (I) Geschichte und Entwickelung der Paleontologie, (II) Die Ueberreste der fossilen Wirbelthiere, (III) Die Wirbelthiere im Kampfe mit der Aussenwelt, (IV) Paläobiologie und Phylogenie. The work is too extensive for an adequate review in this place and it will suffice to say here something of the manner of treatment of the subject matter of the volume. The usual systematic method of compiling a paleontological work is not followed but the subject matter is presented from the standpoint of the adaptation of the animal to its environment and is thus very refreshing to the zoological paleontologists. Such items as the *auditory apparatus of the mosasaurs,* the *parietal organ, expansion of the thorax, dental reduction in the pterosaurs, convergence and parallelism, Todeskampf* are taken at random throughout the work to indicate the nature of the subject matter. Most of the figures are copied from the works of other authors but a few are new. Recent and extinct species are figured side by side when they illustrate the same biologic phenomenon, as for instance on page 438, the recent *Myliobatis aquila* is illustrated side by side with the silurian *Thelodus scoticus.* On page 214 he states that the present writer is mistaken in his correlation of the digits of the Branchiosauria and that the second finger has wrongly been regarded as the first. His reasoning is not adequate to sup-

port his contention. Why should we regard the first finger as having been lost? It would be interesting to have Abel's further views on this matter. The oldest amphibian has but four digits in the hand and they doubtless never had more, but we don't know. His discussion of the *origin of the thumb* is open to question as has been suggested by Doctor Matthew in a previous review of this work. The work as a whole is well printed; the illustrations are clear and show care in selection. The work is, I am sure, a welcome addition to our libraries.

Whatever we may think of the "Arachnid Theory" for the origin of the vertebrates, as outlined in Patten's "Evolution of the Vertebrates and their Kin," we must all acknowledge our debt to Professor Patten for the information on the oldest known vertebrates as outlined in Chapters XX and XXI of that work. Those of us especially who are engaged in the attempt of teaching something of the nature of the oldest known vertebrates must feel grateful to the author for the excellent discussions of these most interesting vertebrates, which he discusses and figures so fully and so beautifully. The text of these two chapters is illustrated with 33 exquisite drawings and photographs based on actual specimens or on the most authoritative works. The writer of these reviews feels a personal debt to Professor Patten for the figures of the left pectoral limb of *Eusthanopteron fordi* (Whiteaves) from the Devonian of Canada. He says of the limb that it

> indicates the way . . . in which the typical skeleton of the pectoral appendage of the tetrapoda has been derived from the biserial pectoral fin of fishes.

We should like to modify the sentence to say *may* instead of *has*, for no one knows whether or not this was the way of the origin of the tetrapodous limb. Restorations of *Cephalaspis, Lasanius, Birkenia, Thelodus, Lanarkia, Drepanaspis* and *Bothriolepis* are given, as well as two photographic pages of specimens of *Bothriolepis* as they occur in the rock; one slab containing nearly a dozen more or less complete specimens. By means of sections Professor Patten has arrived at some conclusions which seem to point, in his opinion, to the arachnoids. The structures he describes are certainly very interesting in their resemblance to arachnid structures. If his interpretation of their value is doubted he has the satisfaction of knowing that no better interpretation has been given. To say that they are characters due to parallelism is beg-

ging the question. If they do not indicate arachnid relationships what do they indicate?

Bertram G. Smith[21] gives a very interesting discussion of "Phylogeny" (in the Amphibia) in his valuable memoir on "Embryology of *Cryptobranchus.*" The keynote to his discussion is contained in the following sentence:

> In the present state of our knowledge it is impossible to reach an unqualified decision of the question under consideration. . . . Whatever light may be shed by future discoveries on the question of the derivation of the amphibia from the crossopterygia or the dipnoi it is clear that the point of origin is not far from either stock; in other words, that the three lines of descent have separated from a common stem at no very great intervals.

The discussion is illustrated by a figure of the pectoral limb of the crossopterygian *Sauripterus taylori* Hall, based on a specimen in the American Museum.

Louise Kellogg[22] has a very interesting paper on the "Pleistocene Rodents of California." The material described is from the cave deposits and the asphalt beds of California. The discussion is intended especially as an elucidation of the possible changes in climatic conditions during the Pleistocene as indicated by the rodent fauna. The species are listed according to the life zones which they indicate; the *Upper Sonoran, Transition* and *Boreal* all being indicated by several species; there being but slight indication of change since the time of deposition of the deposits. Two new subspecies are described.

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[21] *Journal of Morphology,* Vol. 23, No. 3, p. 540 ff.

[22] *Bull. of Dept. Geol. Univ. Calif.,* Vol. 7, No. 8, pp. 151–168.